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Abstract Approved:

Steven H. Sharrow

The effect of defoliation intensity and season on Douglas-fir growth were studied in three replications in the Siuslaw National Forest during 1988-1990. Four intensities of defoliation were applied once in either spring or summer 1988. Stem diameter and canopy area were linearly inversely proportional to the level of defoliation. Defoliation intensity did not affect height growth ($P > 0.05$). Greater losses in height occurred when seedlings were defoliated in spring than in summer.

No differences in predawn and mid-day xylem water potential were observed between trees defoliated in summer or spring 1988. However, in 1989, 25% defoliation reduced mid-day moisture stress whereas 50 and 75% defoliation increased mid-day moisture stress ($P < 0.05$).

Effects of defoliation on length, width, and area of dominant and subdominant twigs as well as number of twigs were separated into different

whorls. As indicated by the sharp slopes of the response surfaces, spring defoliation affected seedlings more ($P < 0.5$) than summer defoliation. No season or intensity effects (except second whorls) on area of dominant twigs were carried over to 1990. No effects ($P > 0.5$) of season or intensity on twig width were observed in 1990. Subdominant twigs were generally more sensitive to defoliation than dominant twigs. Greater losses ($P < 0.5$) in area of subdominant twigs occurred when seedlings were defoliated in spring than in summer. Similar to area, length of twigs continued to respond to defoliation intensity in 1990. Length and width of dominant and subdominant twigs were smaller for spring compared to summer defoliated trees.

Number of twigs were linearly inversely proportional to the level of defoliation intensity in 1989. Intensity did not affect number of twigs in 1990 except second whorls. No effect of defoliation intensity and season on new whorls was detected.

Growth Responses of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) to Defoliation.

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Table of Contents

List of Figures

List of Tables

List of Appendix Tables

Growth Responses of Douglas-fir
(*Pseudotsuga menziesii* [Mirb.] Franco)
to Defoliation

Introduction

A major problem in managing conifer plantations in clear cut areas in the Pacific Northwest is the control of competing vegetation (Newton, 1964; Cleary, 1978). In some cases, controlled livestock grazing is a sound alternative to herbicide use in controlling competing plants (Karl, 1991; Sharrow and Leininger, 1983). Yet, without an understanding the interactions between large herbivores and trees, it is difficult to judge risk of browsing damage to young conifers. There is also a need to estimate how much damage trees can tolerate before individual components of growth are seriously impacted. It has generally been accepted that growth losses following defoliation are often proportional to the amount of foliage removed (Kozlowski, 1969; Kulman, 1971). However, the threshold level at which foliage removal begins to affect tree growth and survival is not well defined. The purpose of this study was to evaluate the effect of lateral branch defoliation on subsequent growth and morphological development of young Douglas-fir trees.

In the summer of 1988, this study began cooperatively with the Alsea Ranger District, Siuslaw National Forest, in Oregon's Coastal Mountain Range. Study plantations were located approximately 16-40 km from Alsea. Study trees were 2-O Douglas-fir planted three years prior to initiation of the study.

Four intensities of artificial defoliation (0, 25, 50, and 75% of new lateral twigs removed) were applied once in either spring or summer 1988 to three replications of 200 trees each. No terminal leaders were removed from any study tree. Subsequent growth trajectories of height, diameter at the base of the tree, diameter at the base of the terminal leader, canopy area, length, width, and area of dominant and subdominant twigs, and number of twigs were measured during the period 1988-1990. Xylem water potential was evaluated during summers 1988 and 1989. Measurements of dominant twigs, subdominant twigs, and number of twigs were grouped according to whorls to evaluate responses within different levels of the crown. Different response surfaces that relate different intensity levels to growth parameters were developed.

CHAPTER 1

Effects of Defoliation on Tree Growth and Development

Effects of Defoliation on Tree Growth and Development

The effect of defoliation on tree growth and development varies between different species. Evergreen conifers such as balsam fir (*Abies balsamea* Mill.), white spruce (*Picea glauca* (Moench) Voss), and hemlock (*Tsuga* sp.), which typically store carbohydrates in their leaves (Ericsson *et al*, 1985), are generally more sensitive to defoliation than are broad-leaved hardwoods. Deciduous conifers such as larch (*Larix* sp.), show a greater resistance to injury from defoliation than do evergreens. Hardwoods can survive three or more years of defoliation and still develop new tissue (Graham, 1929; Kulman, 1971; Knight and Heikknen, 1980). This is mainly due to their relatively large supply of stored food and their ability to replace destroyed tissues rapidly (Graham and Knight, 1965; Knight and Heikknen, 1980). However, more than three successive years of complete defoliation are detrimental even to hardwoods (Graham and Knight, 1965). Within the same species, dominant trees are more resistant than suppressed ones (Graham and Knight, 1965). Trees growing in the open without competition are generally less affected by defoliation than those growing in poor conditions (Graham, 1929; Beal, 1942; Graham and Knight, 1965).

The mechanisms by which trees respond to defoliation are complex in nature because of the myriad of interactions among different growth components. Many factors affect regrowth following defoliation. Some of these factors are: carbohydrate and nitrogen reserves (Ericsson *et al*, 1985), genetic constitution, competition, relative position in reference to micro- or macrotopography (Graham and Knight, 1965; Knight and Heikknen, 1980), available soil nutrients, and precipitation (Knight and Heikknen, 1980). Defoliation results in direct interference with the morphological and physiological processes of trees. It interferes with transpiration, translocation of carbohydrates and organic compounds (Graham, 1929; Kozlowski *et al*, 1991). It affects tree growth by interfering with hormones and regulatory compounds which influence food utilization (Kozlowski, 1969). Reduction in shoot and/or root growth following defoliation are interrelated. If the phloem is damaged, tree injury results from decreased translocation of carbohydrates, organic compounds and growth regulators to the root. Damage to the root system is harmful because it reduces nutrients and water uptake. Shoot growth is reduced because of reduction in mineral uptake and hormones such as cytokinin and gibberellin (Kozlowski *et al*, 1991).

Defoliation can be grouped into two forms: natural and artificial.

Natural Defoliation:

Agents of natural defoliation are segregated into large and small herbivores. Among the small herbivores, insects cause by far the greatest economic loss. Insect defoliators can be separated into four groups according to their feeding habits. These include: leaf miners which feed between the epidermal layers and consume the chlorophyll-bearing tissues, leaving the epidermis intact; skeletonizers which feed on all the leaf except the vascular system; leaf chewers which feed on all leaf tissues (Graham, 1929); and shot-hole feeding larvae which consume all the leaf tissue except the margins (Knight and Heikknen, 1980). No stage in the life cycle of a tree is free from insect attack (Graham, 1952). Physiological changes in woody plants induced by unfavorable conditions, or lack of vigor as trees become overmature (Kozlowski, 1969) are commonly prerequisites for attack by certain insects (Kozlowski *et al*, 1991).

The ability of trees to withstand defoliation is related to their ability to manufacture antiherbivory compounds. Tree resistance to insect attacks is largely biochemical (Kramer and Kozlowski, 1979). Trees producing low amounts of monoterpenes are most susceptible to defoliation (Kozlowski *et al*, 1991). Defense mechanism against insects can be described as static or dynamic. Static defense is characterized by the production of toxic or inhibitory chemicals that make plants less palatable. Dynamic defense is developed in response to attack in order to repel insects or inhibit their development (Berryman, 1986). A comprehensive review on the effects of insect defoliation on growth and mortality of trees was given by Kulman (1971).

Defoliation by large herbivores has been the focus of many researchers; for a comprehensive review on forest grazing see Leininger (1984). Browsing of woody plants by large herbivores is normally restricted to current year's growth, in particular, the early succulent growth (Hill, 1917; Hall *et al,* 1959; Leininger and Sharrow, 1989). Later in the season when needles are mature, browsing effects become minor (Hill, 1917; Leininger and Sharrow, 1989). Repeated early browsing that includes terminal leader removal is damaging and may result in height growth suppression (Hartwell, 1973a). However, if the terminal leader remains intact, browsing of lateral branches is unlikely to adversely affect height growth (Gillingham *et al,* 1976; Hughes, 1976, Sharrow and Leininger, 1983) or basal area (Hughes, 1976). Incidence of terminal leader browsing declines as trees increase in height (Hartwell, 1973b; Pearson, 1931; Leininger and Sharrow, 1989). Browsing damage may also be reduced through the use of large size stock (Dimock, 1970). Some researchers stress the exclusion of livestock from regeneration areas until terminal leaders are beyond animal reach (McDonald, 1986). However, under careful grazing management, through the control of grazing time and distribution, kind, and number of animals, successful establishment and growth of conifers can be achieved (Sharrow and Leininger, 1983; Doescher *et al,* 1987).

The use of large herbivores as a silvicultural tool for controlling competing vegetation has proven to be successful (Doescher and Alejandro, 1985; Doescher *et al,* 1987; Krueger, 1987; Alejandro-Castro, 1988; Sharrow *et al*, 1989). Large herbivores can play an important role in nutrient recycling (Leininger, 1984), and controlling of unwanted vegetation (Sharrow *et al*, 1989). This could lead to tree growth improvement (Hedrick and Keniston, 1966; Sharrow *et al*, 1991), effective increase in the amount of soil moisture available for tree growth (Hedrick and Keniston, 1966; Doescher *et al,* 1989; Karl, 1991), and extending the growing season up to three weeks (Doescher and Alejandro, 1985).

Artificial Defoliation:

Artificial defoliation has long been a tool to study and isolate physiological processes in plants in response to simulated grazing (Kulman, 1971). Although the effect of artificial defoliation is not identical to the browsing by herbivores, it provides a useful means to mimic and quantify natural defoliation. It allows for better estimation of damage, deliberate time selection and relatively more control of defoliation treatments. Factors that influence the effect of defoliation can be separated into four groups: intensity, timing, recurrence, and age of tissue removed.

I. Intensity of defoliation:

Intensity or degree of defoliation refers to the ratio of herbage removed to the original mass (Hodgson, 1979). It has generally been accepted that growth losses in partially defoliated trees are often proportional to the amount of foliage removed (Kozlowski, 1969; Kulman, 1971). However, care must be exercised when viewing this statement because both growth responses and mortality of defoliated trees depend on other factors such as tree species, defoliation severity and time, vigor, site, soil moisture, and prevailing environmental conditions (Kramer and Kozlowski, 1979). In evaluating the effects of defoliation on graminoids, two schools of thoughts have emerged. The first school maintains that grazing benefits plants and may actually stimulate plant production (McNaughton, 1983; Owen and Wiegert, 1976), while others believe that grazing reduces short-term plant productivity (Verkaar, 1986). The previous works of both schools were discussed in two review (Verkaar, 1988; and Belsky, 1986). According to (Belsky, 1986), the beneficial effects of defoliation can be summarized as: increased rate of photosynthesis in residual tissues, increased allocation of current photosynthate to new leaves, reallocation of substrates from other plant parts to the shoots, removal of old, less photosynthetically active tissues, increased light intensity to underlying tissues by opening up the canopy, increased shoot development following removal of apical or dominant meristems, and increased water-use efficiency through the reduction of transpirational surfaces. The application of these concepts to trees has yet to be investigated.

Perusal of the defoliation literature suggests that defoliation intensity is often separated into four levels: light (removal of 30% or less), moderate (removal of 30 to 60%), severe (removal of more than 60%), and complete. It is important to note that researchers may use the same level of defoliation to refer to the removal of either different plant parts or different phenological stages of the same part. This has led to conflicting conclusions in some cases.

Light to moderate defoliation has generally been considered to cause little or no damage to trees. Young trees can sustain 1 to 2 years of light defoliation without substantial growth reduction in height or diameter (Bassman *et al*, 1982). Light defoliation before outplanting has been used to improve field survival. For example, survival was enhanced by defoliating longleaf pine (*Pinus palustris* Mill) needles shortly before outplanting in conditions where seedlings were exposed to significant moisture stress (Barnett, 1984). Such improvement in survival is due to reduction in transpiration (Allen, 1955). In contrast to the foregoing, no advantage of clipping 1-year old needles of slash pine (*Pinus elliottii* Engelm.) to half their original length before outplanting was found (Langdon, 1955). Needle clipping of longleaf pine seedlings immediately before planting reduced vigor and rate of early growth (Derr, 1963).

Individual leaves developing subsequent to partial defoliation were larger than the control and have higher photosynthetic rates (Bassman and Dickmann, 1982). This suggests that the process of assimilate accumulation prior to defoliation operates below its maximum potential (Wareing *et al*, 1968). As a compensation mechanism, conifers are able to increase their photosynthetic rate in the remaining leaves within a few days following partial defoliation (Wareing *et al*, 1968; McGraw *et al*, 1990). This gain in photosynthetic rate is attributed to a boost in the activity of carboxylating enzymes caused by an increase in the supply of cytokinin from the roots to the remaining leaves (Wareing *et al*, 1968).

Unlike partial defoliation, severe defoliation has been regarded by most researchers to be harmful. Height growth is reduced following severe defoliation (Lewis, 1980; Neilsen, 1981). Severe defoliation also reduces diameter growth (Benoit and Blais, 1988), total dry weight (stems, leaves and roots) (Madgwick, 1975), and root growth (Redmond, 1959). Reduction of root growth lowers the plant's ability to meet evapotranspirational demand during hot dry periods. Reduction in root growth following defoliation is attributable to a decreased supply of carbohydrates and other organic compounds (Kozlowski *et al*, 1991).

Complete defoliation on the other hand is the most detrimental of all defoliation levels. A single complete defoliation greatly reduces shoot and cambial growth (Magnoler, 1970). It causes reduction in survival (Beal, 1942) and height and volume increment (Britton, 1988). Survival was significantly reduced when slash pine needles were totally removed within six months after planting (Lewis 1980). In his work with white pine (*Pinus strobus* L.), Lane (1963) noted that no tree survived 100% defoliation. Complete defoliation also reduces leaf, stem, and root weight (McGraw *et al,* 1990). It was reported to lessen root collar extractive (Parker and Houston, 1971) and root starch, suggesting the conversion of starch to sugar (Parker and Houston, 1971; Parker and Patton, 1975).

Researchers disagree about the length of time needed for a tree to recover from defoliation. Some investigators have observed immediate recovery. A complete recovery in the ring width of cork oak the year following defoliation was reported by Magnoler (1970). Other researchers indicated that there is a lag of time between defoliation events and recovery (Blais, 1958; Britton, 1988). A noticeable reduction in growth of the terminal leader was detected two years after complete defoliation of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) mature foliage (Britton, 1988). This suggests a carry over effect. Reduction in radial growth of balsam fir and white spruce that occurred at the earliest in the second year and at the latest in the fourth year following severe defoliation was also reported (Blais, 1958).

II. Timing of defoliation:

The time of the year when defoliation occurs has an impact on subsequent tree growth and development. Conifers are known to withstand a single complete defoliation if it occurs after bud formation (Graham and Knight, 1965). Defoliation of trembling aspen (*Populus tremuloides* Michx.) just before or after bud break did not influence height growth and weight of leaders, however, it resulted in an increase in size and number of leader leaves (Pollard, 1970).

III. Recurrence of defoliation:

The recurrence of defoliation may prevent the plant from rebuilding its reserve carbohydrates, as a result the carbohydrate levels may fall below a critical level. Repeated defoliation may result in progressive reduction in growth, smaller leaves and may ultimately lead to plant death (Kramer and Kozlowski, 1960). Repeated browsing of Douglas-fir seriously reduces height growth (Roy, 1960). Double defoliation during the same season may be damaging, especially if the second one occurs before the formation of the new buds (Graham and Knight, 1965). Sixty percent defoliation of longleaf pine twice in the same growing season was generally worse than a single 90-percent defoliation (Bruce, 1956). Defoliation of young poplars in May and mid July resulted in 60% percent reduction in diameter increment, many unlignified shoots, greater winter damage, and almost one month delay in spring flushing (Kamilovski, 1966). Frequent complete defoliation of mangrove (*Avicennia marina* Vierch.) resulted in death of all plants (Hoshino *et al.,* 1988).

IV. Leaf age:

Different results were obtained when foliage of different ages was removed. Complete removal of leaves of different ages in pines resulted in the least losses when old leaves were removed (Linzon, 1958). Current needles contribute more to shoot growth (Kozlowski and Winget, 1964) and overall growth and survival (Lane, 1963; O'Neil, 1962) than older needles. Stripping needles for ten years, leaving only the most recent two years needles, has lead to a reduction of less than 3% in height growth, 15-45% in volume increment, and 40% in needle production of pine (Burger, 1951).

Pruning:

Pruning of lateral branches has been the practice of foresters for many years to improve wood quality. Pruning of live branches results not only in a reduction of the photosynthetic surface, but also a decrease in the respiratory surface (Kramer and Kozlowski, 1960). It is desirable to remove lower and suppressed branches that consume in respiration all the carbohydrates produced with no contribution to stem growth (Kozlowski, 1971). Moller (1960) reviewed early studies on pruning of Douglas-fir, he concluded that removal of up to one-third the length of the live crown has little effect on height growth. In another study of Douglas-fir, pruning was found to increase height and volume growth (Keller and Thiercelin, 1984). This could be attributed to the fact that height growth normally proceeds at the expense of the carbohydrates produced in the proximal regions of the leader (Kozlowski and Winget, 1964). Stem diameter growth of young radiata pine was reduced by pruning, but the effect was short-lived (Cown, 1973). In contrast, pruning tends to inhibit cambial growth in the stem base (Kramer and Kozlowski, 1979). The effect of pruning depends on intensity, stand density, and crop age before treatment (Brown, 1962). Pruning of 75 percent of green crown resulted in severe depression of diameter growth, with variable recovery time. Removal of 25 percent live crown has little or no effect on diameter or height growth. If depression in growth occurred, it was short lived (Brown, 1962). Wood density was also increased by up to 7 percent for 2 to 3 years after the treatment (Brown, 1962). Best results were obtained with pruning live branches of Norway spruce at 30% of total height (Keller and Thiercelin, 1984).

Literature Cited

Alejandro-Castro, M. 1988. Influence of cattle grazing and forage seeding on establishment of conifers in southwest Oregon. M.S. thesis, Department of Rangeland Resources, Oregon state University, Corvallis.

Allen, R. M. 1955. Foliage treatments improve survival of longleaf pine plantings. J. Forest. 53:724-727.

Barnett, J. P. 1984. Top pruning and needle clipping of container-grown southern pine seedlings. USDA Forest Service-Southern Region, New Orleans Louisiana. P. 39-45.

Bassman, J., D. Dickmann 1982. Effects of defoliation in the developing leaf zone on young Populus X euramericana plants. I. Photosynthetic physiology, growth, and dry weight partitioning. Forest Sci. 28:599-612.

Bassman, J., W. Myers, D. Dickmann and L. Wilson. 1982. Effects of simulated insect damage on early growth of nursery-grown hybrid poplars in northern Wisconsin. Can. J. For. Res. 12:1-9.

Beal, J. A. 1942. Mortality of reproduction defoliated by the red-headed pine sawfly (*Neodiprion lecontei* Fitch). J. of Forestry 40:562-563.

Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. The Am. Nat. 127:878-892.

Benoit, P. and R. Blais 1988. The effect of defoliation by the larch casebearer on the radial growth of tamarack. Forestry chronicle 64:190-192.

Berryman, A. A. 1986. Towards a united theory of plant defense. In: Mechanisms of Woody Plants Defenses Against Insects Search for Pattern (Mattson, W. J., J. Levieux, and Bernard-Dagan, C. ed.) Springer-Verlag. New York. pp. 39-55.

Blais, J. R. 1958. Effects of defoliation by spruce budworm (*Choristoneura fumiferana* Clem.) on radial growth at breast height of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss.). Forestry Chronicle :39-47.

Britton, R. J. 1988. Physiological effects of natural and artificial defoliation on the growth of young crops of lodgepole pine. Forestry 61:166-175.

Brown, G. S. 1962. The importance of stand density in pruning prescriptions. Empire Forest. Rev. 41:246-257.

Bruce, D. 1956. Effect of defoliation on growth of longleaf pine seedlings. Forest. Sci. 2: 31-35.

Burger, H. 1951. Pruning, needle-stripping and increment of young spruce and pine. (German) Mitt. Forstl. VersAnstl, Mariabrunn No. 47:8-16. (Forest. Abstr. 13 No. 156).

Cown, D. J. 1973. Effect of severe thinning and pruning treatments on the intrinsic wood properties of young radiata pine. N. Z. J1, For Sci. 3:379-389.

Derr, H. J. 1963. Needle clipping retards growth of planted longleaf pine. U.S Dept. Agr. Service. Tree Planter's Notes 57:31-33.

Dimock, E. J. 1970. Ten-year height growth of Douglas-fir damaged by Hare and deer. J. of Forestry :285-288.

Doescher, P. S., M. Alejandro 1985. Cattle and establishment of conifer seedlings. Preliminary findings for southwest Oregon. P. 7-10 in Spec. Rep. 743. Agric Exp. Stn., Oreg. State Univ., Corvallis.

Doescher, P. S., S. D. Tesch and M. Alejandro 1987. Livestock grazing: A silvicultural tool for plantation establishment. J. of Forestry 85:29-37.

Doescher, P. S., S. D. Tesch and W. E. Drewien 1989. Water relations and growth of conifer seedlings during three years of cattle grazing on Southwest Oregon plantation. Northwest Sci. 63:232-240.

Ericsson, A. Hehhqvist, C., Langstrom, B., Lasson, S. and Tenow, O. 1985. Effects on growth of simulated and induced shoot pruning by *Tomicus piniperda* as related to carbohydrate and nitrogen dynamics in Scots pine. J. appl. Ecol. 22:105-124.

Gillingham, A. Gg., B. K. Klomp, and S. E. Peterson. 1976. Stock and pasture management for establishment of radiata pine in farmland. P.38-51. In:Proc. N. Z. Grassl. Assoc.

Graham, S. A. and F. B. Knight 1965. Principles of Forest Entomology. (4th Ed.). McGraw-Hill Book Co., New York. 417 p.

Graham, S. A. 1952. Forest Entomology, McGraw-Hill Book Co., Inc.,New York.

Graham, S. A. 1929. Principles of Forest Entomology. (4th Ed.). McGraw-Hill Book Co., New York. 339 p.

Hall, F. C., D. W. Hedrick and Keniston R. F. 1959. Grazing and Douglas-fir establishment in the Oregon white oak type. J. of Forestry 57:98-103.

Hartwell, H. D. 1973a. Effect of deer browsing on height growth of Douglas-fir trees. Dept. of Nat. Res. Notes No. 5.

Hartwell, H. D. 1973b. A comparison of large and small Douglas-fir nursery stock outplanted in potential wildlife damage areas. Dept. of Nat. Res. Notes No. 6

Hedrick, D. W. and R. F. Keniston 1966. Grazing and Douglas-fir growth in the Oregon white oak type. J. of Forestry 64:735-738.

Hill, R. R. 1917. Effects of grazing upon western yellow-pine reproduction in the national forests of Arizona and New Mexico. Bull. No. 580, U.S. Dept. of Agric., Washington, D.C.

Hodgson, J. 1979. Nomenclature and definitions in grazing studies. Grass and Forage Sci. 34:11-18.

Hoshino, M., T. Shinjo and K. Sato. 1988. Utilization of *Avicennia marina* Vierh. as feed for animals. 1. Effect of method and frequency of cutting on the yield and survival of *A. marina*. Japanese J. of Tropical Agric. 32:223-227.

Hughes, R. H. 1976. Response of planted south Florida slash pine to simulated cattle damage. J. Range Manage. 29:198-210.

Kamilovski, M. 1966. Determining the best time to destroy defoliators of poplar. God. Zborn. Zemi. Sum. Fak. Univ. Skopje No. 19 157-86. (Forest. Abstr. 29 No. 2599).

Karl, M. 1991. Effects of prescribed cattle grazing on reforestation in Oregon's Southern Cascades. Ph. D. Diss., Dept. of Rangeland Resources, Oregon State Univ., Corvallis.

Keller, R. and F. Thiercelin. 1984. Pruning of plantations of Norway spruce and Douglas-fir. Revue Forestiere Francaise 36:289-302.

Knight, F. B. and Heikknen H. J. 1980. Principles of Forest Entomology. (5th Ed.). McGraw-Hill Book Co., New York. 461 p.

Kozlowski, T. T. 1969. Tree physiology and forest pests. J. of Forestry. 67:118-122.

Kozlowski, T. T. 1971. Growth and Development of Trees. Vol. 2. Academic Press, New York.

Kozlowski, T. T., Kramer, P. J. and S. G. Pallardy. 1991. Physiological Ecology Woody Plants. Academic Press, Inc. San Diego, California 92101. 657 p.

Kozlowski, T. T., and C. H. Winget. 1964. The role of reserves in leaves, branches, stems and roots on shoot growth of red pine. Am. J. Bot. 51:522-29.

Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of trees. New York:McGraw-Hill Book Co., 642 p.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Kramer, P. J., and T. H. Wetmore. 1943. Effects of defoliation on cold resistance and diameter growth of broad-leaved evergreens. Am. J. Bot. 30:428-31.

Krueger, W. C. 1987. Pacific Northwest forest plantations and livestock grazing. J. of Forestry 85:30-31.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Ann. Rev. of Ent. 16:289-324.

Lane, R. D. 1963. Artificial defoliation of eastern white pine Duplicates some effects of chlorotic dwarf disease. US Forest Service, Research Note CS-16 Central States Exp. Station. Columbus, Ohio. p.6.

Langdon, O. G. 1955. Clipping needles adversely affects survival of south Florida slash pines. U.S. Dept. Agr. Forest. Serv., Southeast Forest. Exp. St. Res. Note 74, Leininger, W. C. 1984. Silvicultural impacts of sheep grazing in Oregon's Coast Range. Ph.D. Dess., Oreg. State Univ., Corvallis. 203 p.

Leininger, W. C. and S. H. Sharrow 1989. Seasonal browsing of Douglas-fir seedlings by sheep. Western J. of Appl. Forestry. 4:73-76.

Lewis, C. E. 1980. Simulating cattle injury to planted slash pine: defoliation. J. Range Manage. 33:345-348.

Linzon, S. N. 1958. The effect of artificial defoliation of various ages of leaves upon white pine growth. Forestry Chronicle 34:50-56.

Madgwick, H. A. I. 1975. Effects of partial defoliation on the growth of *Liriodendron tulipifera* L. seedlings. Ann. Bot. 39:1111-1115.

Magnoler, A. and A. Cambini. 1970. Effects of artificial defoliation on the growth of cork oak. Forest Sc. 16:364-366.

McDonald, P. M. 1986. Grasses in young conifer plantations: hindrance and help. Northwest Sci. 60:271-78.

McGraw, J. B., K. W. Gottschalk, M. C. Vavrek. 1990. Interactive effects of resource availabilities and defoliation on photosynthesis, growth, and mortality of red oak seedlings. Tree Physiology 7:247-254.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Moller, C. M. 1960. The influence of pruning on the growth of conifers. Forestry 33:37-53.

Neilsen, W. A. 1981. Effect of simulated browsing in survival and growth of Pinus radiata (D- Don) seedlings Aust. Forest Res 11: 47-53.

O' Neil, L. C. 1962. Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamn.). Can. J. of Botany 40:273-280.

Owen, D. F. and Wiegert, R. G. 1976. Do consumers maximize plant fitness? Oikos 27:488-492.

Park, J. and R. L. Patton. 1975. Effects of drought and defoliation on some metabolites in roots of black oak seedlings. Can. J. For. Res. 5:457-463.

Parker, J. and Houston, D. 1971. Effects of repeated defoliation on root and root collar extractive of sugar maple trees. Forest Sci. 17:91-95.

Pearson, G. A. 1931. Recovery of western yellow pine seedlings from injury by grazing animals. J. For. 29:876-894.

Pollard, D. W. 1970. Effect of partial defoliation on leader growth. Bi-monthly research notes. Canadian Forestry Service, Dept. of Fisheries and Forestry. 26:10-11.

Redmond, D. R. 1959. Mortality of rootlets in balsam fir defoliated by the spruce budworm. Forest Sci. 4:64-69.

Roy, D. F. 1960. Deer browsing and Douglas-fir Seedling growth in Northwestern California. J. of Forestry 58:518-522.

Sharrow, S. H., W. C. Leininger and B. Rhodes 1989. Sheep grazing as a silvicultural tool to suppress brush. J. Range Manage. 42:2-4.

Sharrow, S. H., W. C. Leininger 1983. Sheep as a silvicultural tool in coastal Douglas-fir forest. P. 219-232 in D.D. Hannaway (ed.), Foothills for food and forests. oregon State Univ., Coll. Agric. Sci. Symp. Series #2. Timber Press, Beaverton, Or.

Sharrow, S. H., W. C. Leininger and K. A. Osman. 1991. Sheep grazing effects on Coastal Douglas-fir forest growth: a ten year perspective. Forest Ecol. and Manage. (in press).

Verkaar, H. J. 1988. Are defoliators beneficial for their host plants in terrestrial ecosystems - a review? Acta Botanica Neerlandica 37:137-152.

Wareing, P. F., M. M. Khalifa and K. J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220:453-457.

CHAPTER 2

Growth Responses of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) to Defoliation

Growth Responses of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) to Defoliation.

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Abstract

The effects of defoliation on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) growth in 3-year old plantations were studied at two sites near Alsea, Oregon during 1988-1990. Four intensities of defoliation (0, 25, 50, and 75% of current year's foliage removed) were applied once in either spring or summer 1988. Tree diameter and canopy area were linearly inversely proportional to the level of defoliation. Defoliation intensity had no effect on tree height growth ($P > 0.05$) throughout the study period. Greater losses ($P < 0.05$) in height occurred when seedlings were defoliated in spring than in summer.

Pre-dawn and mid-day xylem water potentials were monitored using a pressure chamber during summer 1988 and 1989 as an index of tree moisture stress. No differences in predawn and mid-day xylem water potential were observed ($P > 0.05$) between trees defoliated in summer or spring and the control in 1988. However, in 1989, 25% defoliation reduced mid-day moisture

stress ($P < 0.05$), whereas 50% and 75% defoliation increased mid-day moisture stress ($P < 0.05$).

Introduction

Browsing of conifer seedlings by large herbivores is a common silvicultural problem in the Pacific Northwest (Crouch, 1968, Hartwell, 1973). Native herbivores and livestock consume conifer foliage in spite of the presence of tannins, resins, and other antiherbivory compounds commonly present in their tissue. Silvopastural systems that use livestock, as a biological control agent for brush and grass suppression in timber plantations are gaining in popularity (Hedrick and Keniston, 1966; Krueger, 1983; Leininger, 1983; Doescher *et al*, 1987; Alejandro-Castro, 1988; Sharrow *et al*, 1989; Karl 1991). However, livestock may occasionally result in browsing of young seedlings. This has raised the need for quantitative studies to provide reliable estimates of the amount of damage that trees can tolerate and endure.

Considerable research has focused on quantifying growth responses of pines (*Pinus spp.*) to defoliation (Craighead, 1940; Allen, 1955; Bruce, 1956; O' Neil, 1962; Kulman, 1965; Hughes, 1976; Ericsson *et al*, 1980; Lewis, 1980a and 1980b; Neilsen, 1981; Britton, 1988). However, relatively few data have been reported relating defoliation of young Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var *menziesii*) to their subsequent growth and survival. Dearth of this basic information is surprising considering the importance of Douglas-fir as a commercial tree crop, the great amount of research which has been devoted to its silviculture in general, and the frequent interactions between native herbivores or domestic livestock and Douglas-fir trees. The objective of our study was to evaluate relationships between degree and season of defoliation and the subsequent growth and survival of Douglas-fir seedlings.

Study Areas

Three study areas (replications) were located in Oregon's Coastal Mountain Range approximately 16-40 km from Alsea, Oregon (44^0 N, 123^0 W). Study plantations were 3-year old commercial timber stands planted with 2-year old Douglas-fir seedlings (2-O stock type) in 1985. Study areas were selected to avoid locating research in areas which were experiencing grazing use by deer and elk. The elevation of study areas is 80 meters with slopes ranging between 14% and 44%. Climate of the area is maritime with cool, rainy winters and warm, dry summers. Mean annual precipitation is approximately 250 cm most of which falls between October and May (Corliss and Dyrness, 1965). Soils are slick-rock gravelly/loams (Pachic Haplumbrept, Corliss, 1973). Study areas were located within the vine-maple-sward fern (*Acer circinatum* - *Polysticum munitum*) vegetation type which is the most common understory plant community in the local area (Corliss and Dryness, 1965).

Materials and Methods

Defoliation Treatments:

Six hundred Douglas-fir seedlings (200 per replication) were permanently marked with steel tags in May 1988. We selected only healthy seedlings of similar size (mean diameter of selected trees was 14.3 ± 0.13 mm, mean height was 77.2 ± 0.61 cm, and mean canopy area was 2472.9 ± 51.35 cm^2), and which showed no signs of previous browsing damage or disease.

Defoliation was done by hand plucking, and was uniformly distributed over the tree crown. To cover a wide range of defoliation intensities, four defoliation levels 0, 25, 50, and 75% of current year's lateral twigs removed, were applied once in either spring (June) or summer (August) 1988. No terminal leaders were removed from any study tree.

Initial tree diameter (mm) at 20 cm above the soil surface and height (cm) were measured in June 1988, prior to defoliation treatments, using a caliper and meter stick, respectively. Diameter and height of all seedlings were remeasured in December 1988, July 1989, and August 1990. Additional measurements of stem diameter were collected just before bud break in April 1989 and March 1990 to assess winter growth for all seedlings. Basal diameter of terminal leaders was measured at the end of the spring growing season in July 1989 and August 1990. Pre-dawn and mid-day xylem pressure potential

(XPP) were measured in summer 1988 and 1989 to monitor plant moisture stress. Measurements were made at a two-week interval during July-October of 1988 and monthly in 1989 (August - October). Xylem pressure potential of five randomly selected seedlings per treatment was estimated to the nearest 0.05 MPa with a pressure chamber (Waring and Cleary, 1967). To minimize the effect of transpiration, current year's twigs were covered with plastic bags immediately after excision and placed on ice (Turner, 1981). A damp paper towel was placed in the chamber to decrease the vapor pressure deficit. Readings were taken in the field within 45 minutes of sample collection.

Two canopy diameters were measured at right angles, and the canopy area was calculated as:

$$\textit{Canopy Area} = \frac{\textit{Diameter1}}{2} \times \frac{\textit{Diameter2}}{2} \times \pi$$

All seedlings were measured in early June 1988 to establish an initial canopy area. Measurements were taken at the base of the tree to the nearest (cm) using a meter stick. Canopy measurements were repeated in early December 1988, July 1989, and August 1990.

Plantation Management:

High intensity short duration sheep grazing was used as a silvicultural tool for vegetation management (Sharrow *et al*, 1989) during July 1988, and was repeated in August 1989. To prevent animal damage during this experiment, all seedlings were treated with Big Game Repellant (BGR) in July 1988 and August 1989. No damage due to the BGR was observed. To minimize deer damage during winter months, we protected all seedlings in December 1988, using plastic mesh budcaps, which were removed in April 1989. Only 1.2% of the study trees were browsed by sheep or deer during the study.

Data Analysis:

Relative growth rate (RGR) is an overall growth index for comparing rates of growth at different times or among different populations or environments (Ledig, 1974). It allows growth rates to be expressed relative to the amount of growing materials. Relative growth rate was evaluated in addition to the absolute growth, because it decreases the effect of initial size differences and is a good measure of growth efficiency (Ledig, 1974). Relative growth of diameter, height, and canopy area were calculated following the procedure of Evans (1972):

$$RGR = \frac{\ln d_i - \ln d_{i-1}}{t_i - t_{i-1}} \times 100$$

where:

RGR = Relative Growth Rate.

d_{i-1} and d_i = Tree diameter at the beginning and the end of the sampling period.

t_{i-1} and t_i = The first and second sampling time.

ln = Natural logarithm.

Data were analyzed as a 4 X 2 factorial arrangement of treatments in a randomized complete block design with three areas as blocks (Snedecor and Cochran, 1989). Treatments (four intensities, two seasons of defoliations) were randomly assigned to the seedlings within each block. Treatment effects on tree height, diameter, and canopy area were adjusted for initial tree size by covariance. The following model (Steel and Torrie, 1980) was used:

$$Y_{ijk} = \mu + \rho_i + \alpha_j + \tau_k + (\alpha\tau)_{jk} + \beta(X_{ijk} - \bar{X}...) + \epsilon_{ijk}$$

Where:

Y_{ijk} = dependent variable.
μ = overall mean.
ρ_i = effect of the ith block.
α_j = added effect of the jth level of season.
τ_k = added effect of the kth level of intensity.
$(\alpha\tau)_{jk}$ = added effect of the interaction between season and intensity.
β = regression coefficient.
X = independent or covariable.
ϵ_{ijk} = random error.

Upon detection of significant treatment differences, means were separated by Fisher's protected LSD procedure (Snedecor and Cochran, 1989). Response surfaces for significant intensity effects were developed using least squares regression procedures (Netter and Wasserman, 1989). Best fit response surfaces were selected from linear, quadratic, and cubic models using SAS (SAS Institute, 1990). Best fit models were those which had the lowest Mallow's Cp, highest R^2 and whose individual regression coefficients were all significantly different from zero.

Results and Discussion

Survival:

Survival was excellent throughout the course of the experiment with only 0.3% tree mortality during the study period.

Responses to Defoliation Intensity:

The intensity X season interaction was not significant ($P > 0.05$) for any parameter measured. Therefore, results will focus on the main effects of defoliation intensity and season on tree growth. Tree basal diameter, terminal leader diameter, and tree canopy area all displayed similar response to defoliation intensity. Average tree diameter on all sampling dates was linearly inversely proportional to the intensity of defoliation (Figure 2-1). The rate of reduction in diameter (β_1) as defoliation increased became more pronounced with time, ranging between 0.0051-0.0529 mm of diameter for each additional 1% defoliation during 1988-1990. Seventy five percent defoliation caused a reduction of 1.5, 7.8, and 8.0 percent in diameter growth compare to the control during summer 1988, 1989, and 1990, respectively. Fifty percent defoliation reduced diameter growth by 1.0, 6.4, and 6.5 percent compared to the control during summer 1988, 1989, and 1990, respectively. Twenty five percent defoliation had little effect on diameter growth. Similar results were obtained for pines by (Kulman, 1971; Kozlowski, 1969). The relatively low slopes of our response surfaces suggest that young Douglas-fir trees are quite tolerant of lateral branch defoliation. Similarly, Lewis (1980a and 1980b) indicate that slash pine (*Pinus elliottii* Engelm.) can withstand considerable injuries before any real damage occurred.

Intensity of defoliation had less effect on diameter of terminal leaders than on basal diameters measured in summer 1989 and 1990. Rate of reduction in terminal leader diameter was similar both years being approximately 1.2% of terminal leader diameter for each unit increase in defoliation intensity (Figure 2-2). Canopy area also decreased with increasing defoliation intensity. The effect of defoliation on canopy area became more pronounced with time since defoliation, probably reflecting the geometric nature of conifer tree growth (Figure 2-3). Average canopy per tree declined by 15.1, 13.0, and 12.1% for December 1988, July 1989, and August 1990 measurements, respectively, when 75% defoliation was applied compare to the control.

In contrast to basal diameter, average tree height (Table 2-1) did not differ between defoliation intensities on any sampling date ($P > 0.05$). This could be related to the differences in the nature of growth for height and diameter. Height growth is determinate (Kramer and Kozlowski, 1979) while diameter growth is indeterminate in nature. Diameter, therefore, is more highly dependent on current-year resource availability, especially water

(Kramer and Kozlowski, 1979) than is height growth. Height and diameter also differ in their source-sink relationships. Diameter growth has lower priority for photosynthate allocation than shoot growth. It occurs once the resource demands of foliage and root growth have been accommodated (Waring, 1987). Thus, the diameter growth of stressed seedlings will be affected before the height growth.

Figure 2-1. Response surface relating defoliation intensity (%) to average stem diameter (mm) during 1988-90.

April 1989:
Average Diameter = 20.84 - 0.0156 Intensity
R^2=0.96 Cp=3.0

July 1989:
Average Diameter = 27.83 - 0.0348 Intensity
R^2=0.95 Cp=2.8

March 1990:
Average Diameter = 30.08 - 0.0355 Intensity
R^2=0.95 Cp=3.4

August 1990:
Average Diameter = 41.59 - 0.0529 Intensity
R^2=0.94 Cp=1.4

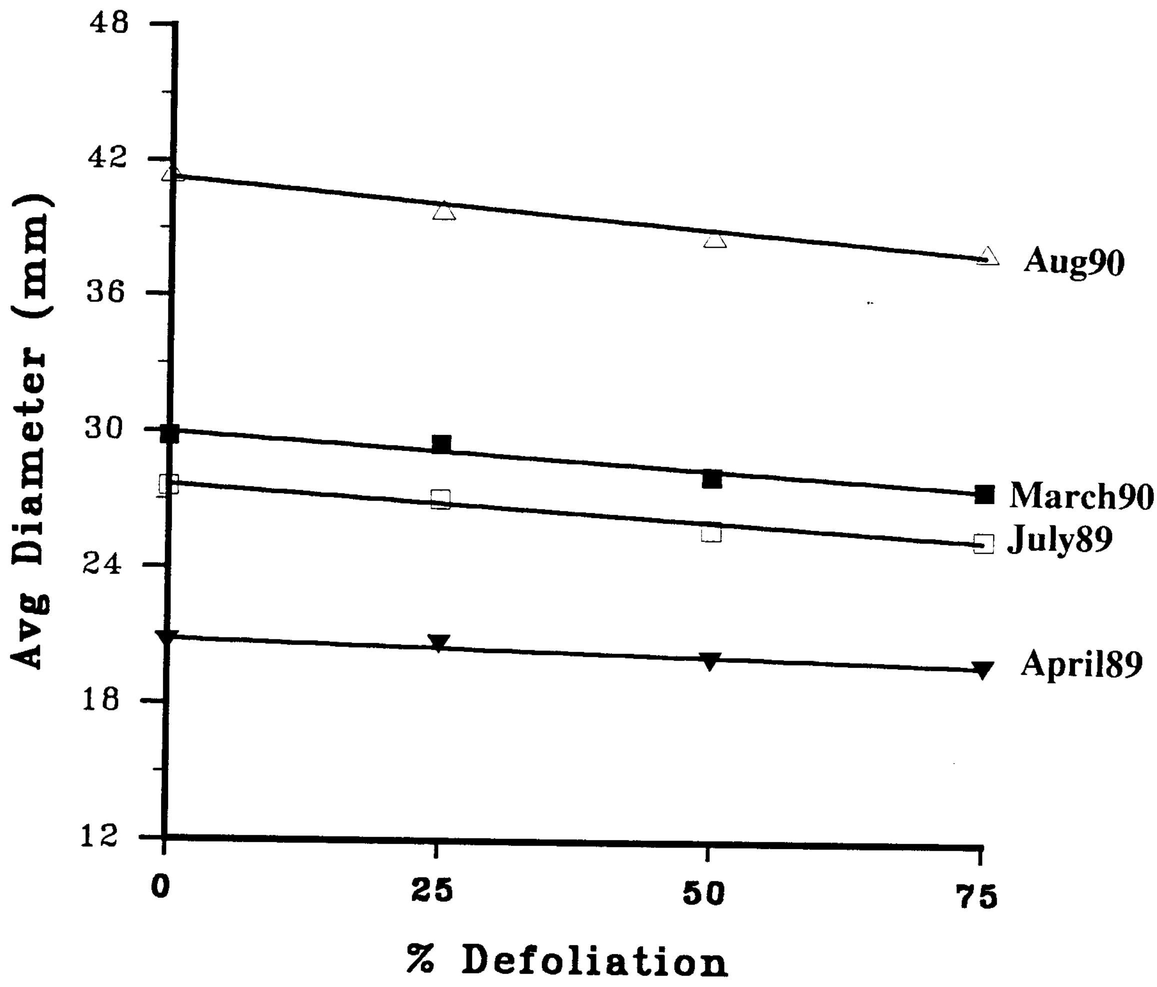
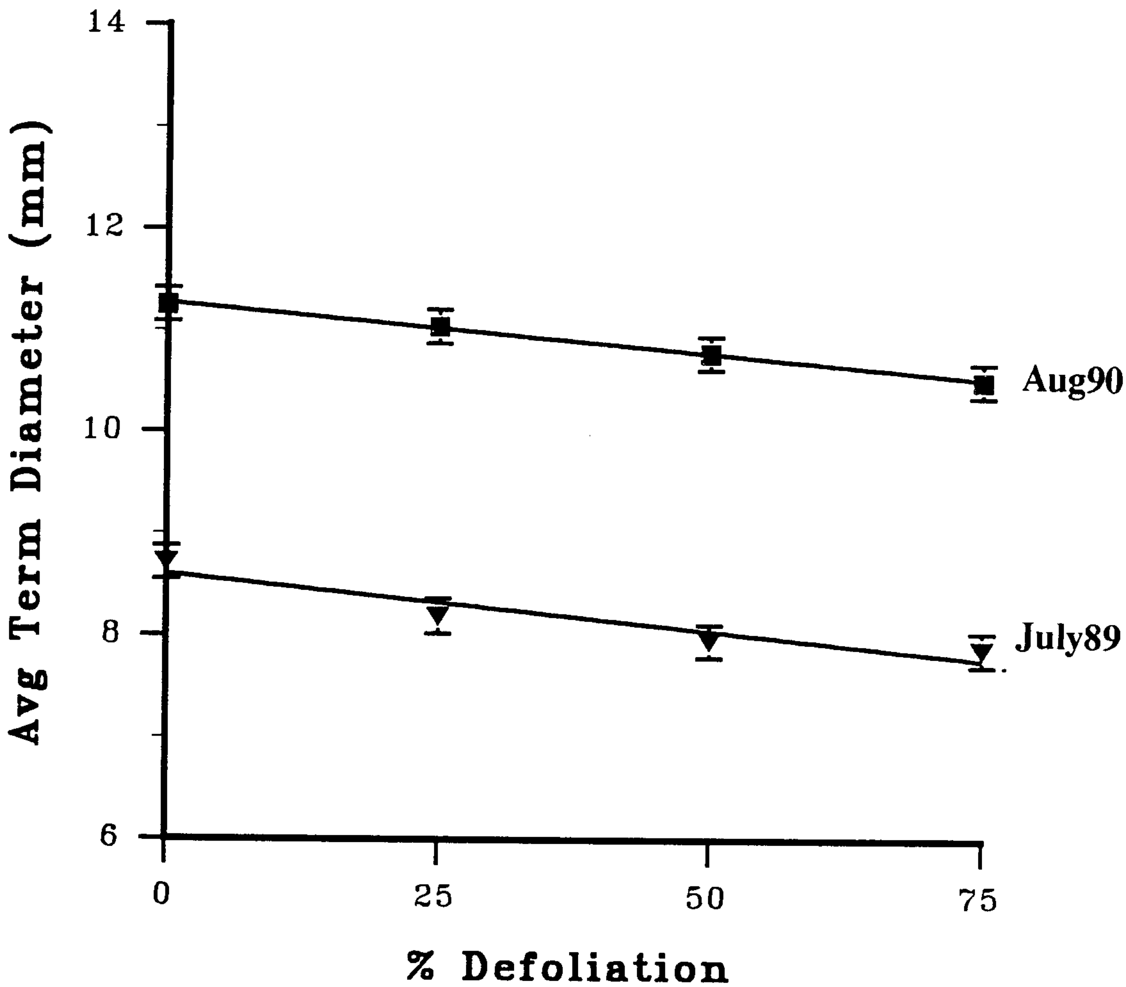

48
42
36
30
24
18
12
Avg Diameter (mm)
Aug90
March90
July89
April89
0
25
50
75
% Defoliation

Figure 2-1.

Figure 2-2. Response surface relating defoliation intensity (%) to average diameter of the terminal leader (mm) during 1988-90.

July 1989:
Average Diameter = 8.54 - 0.0124 Intensity
R^2=0.90 Cp=2.1

August 1990:
Average Diameter = 11.27 - 0.011 Intensity
R^2=0.90 Cp=1.2



14
12
10
8
6
Avg Term Diameter (mm)
0
25
50
75
% Defoliation
Aug90
July89

Figure 2-2.

Figure 2-3. Response surface relating defoliation intensity (%) to average canopy area (cm^2) during 1988-90.

December 1988:
Average Diameter = 3510.77 - 6.7 Intensity.
R^2=0.73 Cp=3.0

July 1989:
Average Diameter = 7945.41 - 13.2 Intensity
R^2=0.81 Cp=3.0

August 1990:
Average Diameter = 16115.83 - 26.9 Intensity
R^2=0.75 Cp=3.0

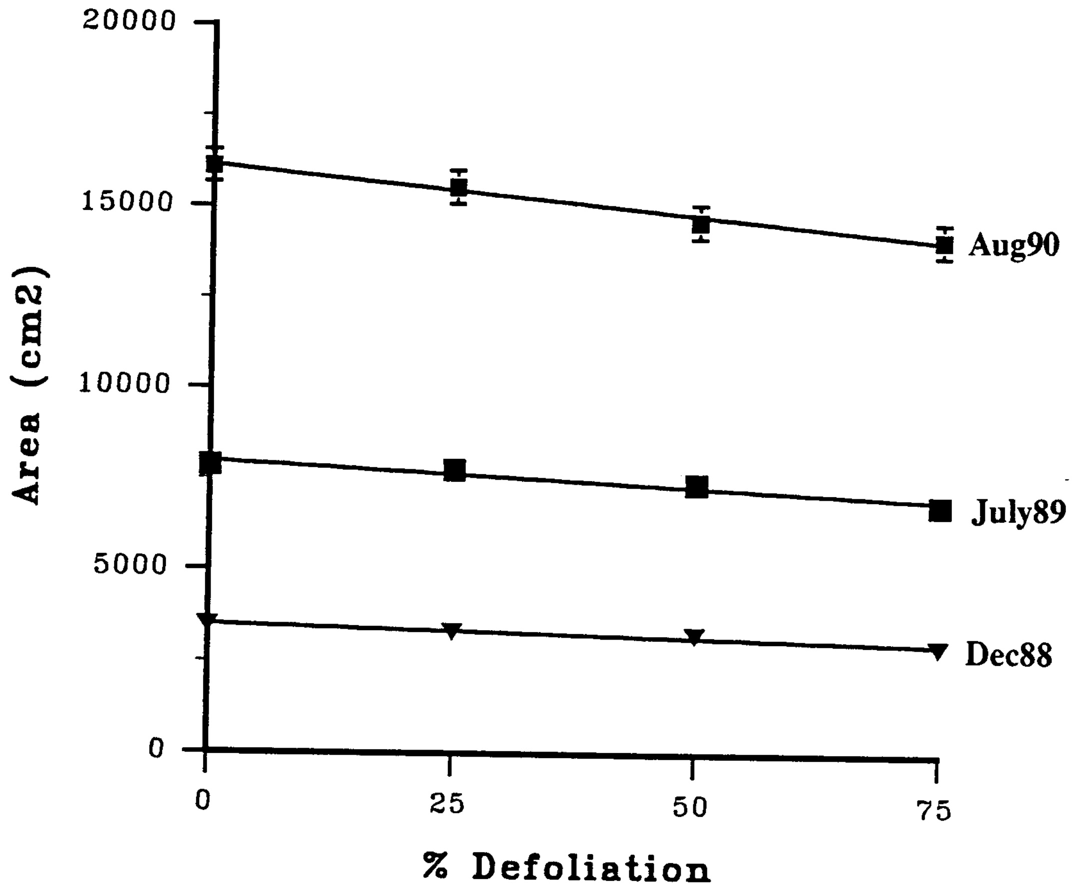

20000
15000
10000
5000
0
Area (cm2)
0
25
50
75
% Defoliation
Aug90
July89
Dec88

Figure 2-3.

Table 2-1. Effects of Defoliation Intensity on Douglas-fir Average Height (cm ± SE) 1988-1990.

Date	Defoliation Intensity			
	0%	25%	50%	75%
12/19/88	121.53 (0.98)a	120.97 (1.00)a	122.36 (0.98)a	121.46 (0.99)a
07/11/89	174.97 (2.13)a	172.34 (2.18)a	170.64 (2.14)a	169.45 (2.15)a
08/11/90	257.64 (3.38)a	252.00 (3.45)a	251.62 (3.39)a	246.83 (3.40)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Relative Growth Rates:

Similar to their absolute values, the relative growth rates RGR for tree basal diameter (Table 2-2) and canopy area (Table 2-3), decreased as defoliation intensity increased during 1988 and 1989, respectively. However, contrary to their absolute values, defoliation intensity effects on RGR decreased with time since defoliation. The effects on basal diameter RGR were limited to the first growing seasons following defoliation (1989), while intensity only affected canopy RGR during the year of defoliation (1988). Apparently the tendency of treatment effects on tree basal diameter and canopy area to increase with time since defoliation reflects the geometric nature of tree growth in which initial treatment effects on growth are magnified with time as trees grow relative to their instantaneous size. Similar to tree height, height RGR did not differ ($P > 0.05$) between defoliation intensity treatments (Table 2-4).

Table 2-2. Effects of Defoliation Intensity on Douglas-fir Relative Diameter Growth Rates (%/day ± SE) 1988-1990.

Period	Defoliation Intensity			
	0%	25%	50%	75%
12/19/88	0.116 (0.005)a	0.118 (0.005)a	0.112 (0.005)a	0.108 (0.005)a
04/23/89	0.110 (0.004)a	0.101 (0.004)ab	0.089 (0.004)bc	0.083 (0.004)c
07/11/89	0.357 (0.010)a	0.336 (0.010)ab	0.316 (0.010)b	0.313 (0.010)b
03/17/90	0.031 (0.002)a	0.035 (0.002)a	0.036 (0.002)a	0.031 (0.002)a
08/11/90	0.221 (0.005)a	0.198 (0.005)a	0.217 (0.005)a	0.215 (0.005)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-3. Effects of Defoliation Intensity on Douglas-fir Relative Canopy Growth Rates (%/day ± SE) 1988-1990.

	Defoliation Intensity			
Period	0%	25%	50%	75%
12/19/88	0.190 (0.017)a	0.159 (0.017)a	0.149 (0.017)a	0.095 (0.017)b
07/11/89	0.385 (0.016)a	0.406 (0.016)a	0.386 (0.016)a	0.419 (0.016)a
08/11/90	0.189 (0.005)a	0.181 (0.005)a	0.182 (0.005)a	0.194 (0.005)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-4. Effects of Defoliation Intensity on Douglas-fir Relative Height Growth Rate (%/day ± SE) 1988-1990.

	Defoliation Intensity			
Period	0%	25%	50%	75%
12/19/88	0.231 (0.004)a	0.225 (0.004)a	0.232 (0.004)a	0.231 (0.004)a
07/11/89	0.175 (0.004)a	0.170 (0.004)a	0.160 (0.004)a	0.161 (0.004)a
08/11/90	0.098 (0.002)a	0.097 (0.002)a	0.100 (0.002)a	0.095 (0.002)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Responses to Season of Defoliation:

Average tree diameter (Table 2-5) was lower for spring defoliated than for summer defoliated or undefoliated trees prior to bud break in April 1989, the growing season following defoliation, but similar thereafter. Season of defoliation had no effect ($P > 0.05$) on basal diameter RGR (Table 2-6). Effects of defoliation season on canopy cover values (Table 2-7) were evident in December 1988 when summer defoliated trees had 14% less canopy than spring defoliated and undefoliated trees. Canopy area RGR in 1988 was reduced by summer defoliation (Table 2-8). Seedlings defoliated in summer continued to be taller than those defoliated in spring during 1988 and 1989 (Table 2-9).

The response of height and diameter may reflect the nature of their timing of growth. In the Coast Range, Douglas-fir foliage and leader growth generally stops in August long before cambial growth which continues on until October (Emmingham, 1977). In our experiment summer defoliation was carried out in August after the cessation of leader and lateral branch growth. Thus foliage removed by summer defoliation was previously available to the tree during the most suitable time of year for rapid photosynthesis and tree growth.

Table 2-5. Effects of Season of Defoliation on Douglas-fir Average Basal and Terminal Diameter (mm ± SE) 1988-1990.

	Season		
Date	Control	Spring	Summer
Average Basal Diameter			
12/19/88	17.95 (0.22)a	17.59 (0.22)a	18.28 (0.22)a
04/23/89	20.63 (0.27)a	19.80 (0.27)a	20.59 (0.27)a
07/11/89	27.48 (0.45)a	25.69 (0.44)a	26.60 (0.44)a
03/17/90	29.71 (0.48)a	28.01 (0.47)a	28.90 (0.47)a
08/11/90	41.32 (0.76)a	39.67 (0.74)a	39.30 (0.76)a
Average Terminal Diameter			
07/11/89	8.68 (0.24)a	7.83 (0.23)a	8.20 (0.23)a
08/11/90	11.23 (0.24)a	10.80 (0.23)a	10.76 (0.23)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-6. Effects of Season of Defoliation on Douglas-fir Relative Diameter Growth Rates (%/day ± SE) 1988-1990.

	Season		
Period	Control	Spring	Summer
12/19/88	0.117 (0.003)a	0.105 (0.005)a	0.122 (0.004)a
04/23/89	0.109 (0.009)a	0.092 (0.010)a	0.092 (0.008)a
07/11/89	0.358 (0.017)a	0.326 (0.011)a	0.319 (0.016)a
03/17/90	0.031 (0.003)a	0.035 (0.002)a	0.034 (0.003)a
08/11/90	0.222 (0.008)a	0.216 (0.010)a	0.217 (0.006)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-7. Effects of Season of Defoliation on Douglas-fir Average Canopy ($cm^2 \pm SE$) 1988-1990.

	Season		
Date	Control	Spring	Summer
12/19/88	3520.1 (127.4)a	3303.2 (130.4)a	3034.2 (129.5)b
07/11/89	7905.0 (284.8)a	7336.5 (296.5)a	7266.6 (289.6)a
08/11/90	16224.7 (633.7)a	14398.3 (648.9)a	14663.4 (625.0)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-8. Effects of Season of Defoliation on Douglas-fir Relative Canopy Growth Rates (%/day ± SE) 1988-1990.

	Season		
Period	Control	Spring	Summer
12/19/88	0.179 (0.023)a	0.177 (0.023)a	0.098 (0.023)b
07/11/89	0.381 (0.023)a	0.381 (0.023)a	0.412 (0.023)a
08/11/90	0.185 (0.007)a	0.180 (0.007)a	0.185 (0.007)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-9. Effects of Season of Defoliation on Douglas-fir Average Height (cm ± SE) and Relative Height Growth Rates (%/day ± SE) 1988-1990.

	Season		
Date	Control	Spring	Summer
12/19/88	121.33 (1.7)ab	120.24 (1.4)b	123.09 (1.4)a
07/11/89	174.75 (1.8)a	167.52 (1.7)b	174.24 (1.8)a
08/11/90	257.38 (2.8)a	247.81 (2.7)b	252.67 (2.9)a
	Relative Height Growth Rates		
12/19/88	0.232 (0.006)a	0.223 (0.006)b	0.239 (0.006)a
07/11/89	0.178 (0.006)a	0.162 (0.006)a	0.169 (0.006)a
08/11/90	0.097 (0.003)a	0.099 (0.003)a	0.094 (0.003)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Xylem Water Potential (Ψ):

Neither defoliation season nor intensity affected tree water stress in 1988 (Tables 2-10 and 2-11). The year following defoliation, in 1989 (Table 2-12), 25% defoliation reduced mid-day moisture stress (less negative xylem water potential, $P > 0.05$). Fifty and seventy five percent defoliation increased mid-day moisture stress ($P < 0.05$). Twenty five percent defoliation may reduce moisture stress by reducing canopy surface exposed to evapotranspiration. Similar studies with pines indicated that partial defoliation reduced transpirational water use by 30 percent (Allen, 1955). Presumably, 50% to 75% defoliation of Douglas-fir trees reduces root growth as has been observed for balsam fir (Redmond, 1959), and mycorrhizal levels (Gehring and Whitham, 1991) . Reduction of root mass would be expected to lower the plant's ability to meet evapotranspirational water demand during hot dry periods.

Table 2-10. Douglas-fir Pre-Dawn Xylem Water Potential (MPa ± SE) 1988.

Season	Sampling Date				
	July 2nd	July 16th	July 30	Aug 13th	Average
Control	-0.715(0.155)bd	-0.497(0.132)ac	-0.647(0.044)ab	-0.970(0.142)ed	(-0.707)a
Spring	-0.710(0.035)bd	-0.472(0.024)a	-0.649(0.043)bc	-0.872(0.051)e	(-0.673)a
	Aug 23	Sept 10th	Oct 2nd	Oct 17th	
Control	-0.877(0.067)b	-1.107(0.048)cd	-0.433(0.015)a	-0.497(0.068)a	(-0.728)a
Summer	-0.932(0.045)bd	-1.124(0.024)c	-0.433(0.016)a	-0.456(0.029)a	(-0.736)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-11. Douglas-fir Mid-day Xylem Water Potential (MPa ± SE) 1988.

Season	July 2nd	July 16th	July 30	Aug 13th	Average
Control	-1.110(0.050)a	-1.747(0.073)b	-1.853(0.067)b	-2.027(0.063)d	(-1.684)b
Spring	-1.161(0.038)a	-1.691(0.018)b	-1.906(0.051)b	-1.823(0.080)b	(-1.645)b
	Aug 23	Sept 10th	Oct 2nd	Oct 17th	
Control	-2.080(0.050)b	-2.240(0.058)b	-2.173(0.066)b	-1.470(0.119)a	(-1.991)a
Summer	-2.108(0.048)b	-2.198(0.030)b	-2.229(0.037)b	-1.443(0.089)a	(-1.994)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Table 2-12. Douglas-fir Pre-Dawn and Mid-day Xylem Water Potential (MPa ± SE) 1989.

	Defoliation Intensity			
Time	0%	25%	50%	75%
Pre-Dawn	-0.555 (0.023)a	-0.560 (0.022)a	-0.542 (0.023)a	-0.580 (0.029)a
Mid-day	-1.985 (0.046)c	-1.753 (0.059)d	-2.117 (0.047)b	-2.292 (0.032)a

Means within a row followed by the same letter do not differ ($P \leq 0.05$, Fisher's Protected LSD).

Conclusions

The direct effect of season of defoliation on diameter and canopy area is limited to the year of treatment. However, a residual effect of treatments reflected differences in tree size at the end of 1988. Spring defoliation was more detrimental to subsequent plant growth than summer defoliation. Deer (Crouch, 1968) and livestock (Leininger and Sharrow, 1989) browsing on Douglas-fir trees is more commonly encountered in spring, when new tree growth has not yet hardened off, than in summer. However, the relatively shallow slopes of our response surfaces relating tree growth to defoliation intensity indicated that young Douglas-fir are very tolerant of lateral browsing regardless of season. Loss of terminal leaders, however, may significantly reduce both tree height and diameter growth (Sharrow *et al*, 1991).

Current prescription grazing recommendations for using livestock as a tool to control competing vegetation in Pacific Coastal Douglas-fir plantations (Sharrow *et al*, 1989) are designed to minimize browsing of trees by reducing grazing pressure in the spring. Our data suggest that grazing prescriptions and wildlife damage control programs should concentrate on protection of terminal leaders from browsing. Seedlings whose terminal leader is above the reach of herbivores or whose leader is protected (either chemically mechanically) are unlikely to be damaged by browsing.

Acknowledgements

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Literature Cited

Alejandro-Castro, M. 1988. Influence of cattle grazing and forage seeding on establishment of conifers in southwest Oregon. M.S. thesis, Department of Rangeland Resources, Oregon state University, Corvallis.

Allen, R. M. 1955. Foliage treatments improve survival of longleaf pine plantings. J. of Forestry. 53:724-727.

Britton, R. J. 1988. Physiological effects of natural and artificial defoliation on the growth of young crops of lodgepole pine. Forestry 61:166-175.

Bruce, D. 1956. Effect of defoliation on growth of longleaf pine seedlings. Forest. Sci. 2: 31-35.

Corliss, J. F. 1973. Soil survey - Alsea area, Oregon. U. S. Govt. Printing Office, Washington, D.C.

Corliss, J. F., and C. T. Dyrness. 1965. A detailed soil-vegetation survey of the Alsea area in the Oregon Coast Range. P. 457-483. In: C.T. Youngberg (ed.).Forest soil relationships in North America. Oregon State Univ. Press, Corvallis.

Craighead, F. C. 1940. Some effects of artificial defoliation on pine and larch. J. of Forestry 38:885-888.

Crouch, G. L. 1968. Spring-season deer browsing of Douglas-fir on the capitol forest in western washington. US Forest Service Research Note. PNW-84.

Doescher, P. S., S. D. Tesch and M. Alejandro. 1987. Livestock grazing: A silvicultural tool for plantation establishment. J. of Forestry 85:29-37.

Emmingham, W. H. 1977. Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. Can. J. For. Res. 7:154-164.

Ericsson, A., S. Larsson, and O. Tenow. 1980. Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pine. J. of Appl. Ecol. 17:747-76

Evans, G. C. 1972. The quantitative analysis of plant growth. Univ. of California Press Berkeley.

Gehring, C. A. and T. G. Whitham. 1991. Herbivore-driven mycorrhizal mutualism in insect-susceptible pinyon pine. Nature 353:556-557.

Hartwell, H. D. 1973. Effect of deer browsing on height growth of Douglas-fir trees. Dept. of Nat. Res. Notes No. 5.

Hedrick, D. W. and R. F. Keniston. 1966. Grazing and Douglas-fir growth in the Oregon white oak type. J. of Forestry 64:735-738.

Hughes, R. H. 1976. Response of planted south Florida slash pine to simulated cattle damage. J. Range Manage. 29:198-210.

Karl, M. 1991. Effects of prescribed cattle grazing on reforestation in Oregon's Southern Cascades. Ph. D. Diss., Dept. of Rangeland Resources, Oregon State Univ., Corvallis.

Kozlowski, T. T. 1969. Tree physiology and forest pests. J. of Forestry. 67:118-122.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Krueger, W. C. 1983. Cattle grazing in managed forests, p. 29-41. In: B. F. Roche and D. M. Baumgartner (eds.), Proc. of Forestland Grazing Symposium, Washington State Univ., Pullman.

Kulman, H. M. 1965. Effects of artificial defoliation of pine on subsequent shoot and needle growth. Forest Sci. 11:90-98.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Ann. Rev. of Ent. 16:289-324.

Ledig, F. T. 1974. Concepts of growth analysis. P.166-182 in Proc. 3rd North Am. For. Bio. workshop. Coll. of For. and Natural Resource. Colorado State Univ., Fort Collins.

Leininger, W. C. 1983. Silvicultural impacts of sheep grazing in Oregon's Coast Range. Ph.D. Dess., Oreg. State Univ., Corvallis. 203 p.

Leininger, W. C. and S. H. Sharrow 1989. Seasonal browsing of Douglas-fir seedlings by sheep. Western J. of Appl. Forestry. 4:73-76.

Lewis, C. E. 1980a. Simulating cattle injury to planted slash pine: defoliation. J. Range Manage. 33:345-348.

Lewis, C. E. 1980b. Simulating cattle injury to planted slash pine: Combinations of defoliation, browsing, and trampling. J. Range Manage. 33:340-345.

Neilsen, W. A. 1981. Effect of simulated browsing in survival and growth of Pinus radiata (D- Don) seedlings Aust. Forest Res 11: 47-53.

Neter, J., and W. Wasserman. 1989. Applied linear statistical models. Richard D. Irwin, Inc., Homewood,Il.

O' Neil, L. C. 1962. Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamn.). Can. J. of Botany 40:273-280.

Redmond, D. R. 1959. Mortality of rootlets in balsam fir defoliated by the spruce budworm. Forest Sci. 4:64-69.

Running, S. W. 1976. Environmental control of leaf water conductance in conifers. Can. J. of For. Res. 6:104-112.

SAS Institute Inc. 1990. SAS/STAT Guide for personal computers. Version 6.03 ed. SAS Institute Inc., Cary, NC.

Sharrow, S. H., W. C. Leininger and B. Rhodes. 1989. Sheep grazing as a silvicultural tool to suppress brush. J. Range Manage. 42:2-4.

Sharrow, S. H., W. C. Leininger and K. A. Osman. 1991. Sheep grazing effects on Coastal Douglas-fir forest growth: a ten year perspective. Forest Ecol. and Manage. (in press).

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods. 8th Edition. The Iowa State Univer. Press, Ames, Iowa.

Steel, R. G. O. and J. H. Torrie. 1980. Principles and procedures of statistics. Second edition. McGraw-Hill book company. New York.

Turner, N. C. 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil:339-366.

Waring, R. H., and B. D. Cleary. 1967. Plant moisture stress: Evaluation by pressure bomb. Science 155:1248-1254.

Waring, R. H. 1987. Characteristics of trees predisposed to die. BioScience, 37:569-574.

CHAPTER 3

Morphological Responses of Douglas-fir

(Pseudotsuga menziesii [Mirb.] Franco)

to Defoliation

Morphological Responses of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). to Defoliation

Abstract

The effect of defoliation intensity and season on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) morphology were studied during 1988-1990. Effects of defoliation on length, width and area of dominant and subdominant twigs and number of twigs were grouped into different whorls. Response surface models relating defoliation intensity (%) to area and length of dominant and subdominant twigs and number of twigs were developed. The results indicated a gradient of response in area, length, width and number of twigs within the crown. As indicated by the sharp slopes of the response surfaces, spring defoliation affected seedlings more ($P < 0.5$) than summer defoliation. No season or intensity effects (except second whorls) on area of dominant twigs were carried over to 1990. Defoliation effects upon dominant twig areas accrued mainly from differences in twig length and both respond in similar manner in 1989. No effects ($P > 0.5$) of season or intensity on dominant twig width were observed in 1990. Season or intensity of defoliation did not affect any of dominant twig parameters in newly produced whorls in 1990.

Subdominant twigs were generally more sensitive to defoliation than dominant twigs, and defoliation effects were still evident two years after treatment. Greater losses ($P < 0.5$) in area of subdominant twigs occurred when seedlings were defoliated in spring than in summer. Length of twigs continued to respond to defoliation in 1990. Length and width of dominant and subdominant twigs were smaller for spring compared to summer defoliated trees.

Number of twigs were linearly inversely proportional to the level of defoliation intensity in 1989. Intensity did not affect number of twigs in 1990 except second whorls. No effect of defoliation intensity and season on new whorls was detected.

Introduction

The response of trees to defoliation is of both biological and practical interest as it can provide insight into resource partitioning within browsed trees as well as be reflected in subsequent tree productivity and form. Use of prescription livestock grazing as a biological control for unwanted forest understory vegetation is gaining in popularity in the Pacific Coastal Region of the United States and Canada. Browsing of young conifers by native herbivores, primarily deer and elk, is a silvicultural concern for young Douglas-fir plantations throughout this region (Crouch, 1968, Hartwell, 1973). Unfortunately, reliable quantitative data relating known levels of defoliation to subsequent Douglas-fir tree form is not presently available.

Most defoliation studies have focused on general responses of trees to defoliation on a whole tree basis (Bruce, 1956; Hughes, 1976; Bassman *et al*, 1982). Growth losses in partially defoliated trees are often proportional to the intensity of defoliation (Kozlowski, 1969; Kulman, 1971). Components of tree growth are often affected differentially with height growth being less sensitive to defoliation than is diameter growth (Hughes, 1976; Rook and Whyte, 1976; Ericsson *et al*, 1980). There are currently few data which describes the morphological response of different tree parts to defoliation. Leaves at different locations in the crown respond differently to defoliation (Ericsson *et al*, 1980). The position of leaves in the crown affects their physiological activities (Larson and Gordon, 1969). Leaves in lower stems are known to mature faster and start exporting photosynthate when demands of young seedlings are high. In contrast, leaves at higher stem positions mature more slowly (Larson and Gordon, 1969). Large sinks have higher competitive potential for photosynthate than smaller ones (Waring and Patrick, 1975). Presumably different physiological attributes of plant organs will be reflected in different morphological response to defoliation.

The objective of the study was to investigate the effects of defoliation intensity and season on the following morphological traits: length, width and area of Douglas-fir dominant and subdominant twigs and the number of twigs in each tree whorl.

Study Areas

Trees used in this work were Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees growing in three replications in the Siuslaw National Forest in Oregon's Coastal Mountain Range, USA. The study areas were located approximately 16-40 km southwest of Alsea, Oregon (44° N, 123° W). Study trees were (2-0, stock type) planted in 1985. The elevation is 80 meters with slopes ranging between 14 and 44%. Climate of the area is characterized by cool rainy winters and warm, dry summers. Mean annual precipitation is approximately 250 cm most of which falls between October and May (Corliss and Dyrness, 1965). Soils are composed of slick-rock gravelly/loams (Pachic Haplumbrept, Corliss, 1973). The major coniferous species is Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var *menziesii*), with considerable amounts of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red-cedar (*Thuja plicata* D. Don). Major hardwoods on the site include red alder (*Alnus rubra* Nutt.), vine maple (*Acer circinatum* Pursh) and big leaf maple (*Acer macrophyllum* Pursh) (Corliss and Dyrness, 1965).

Materials and Methods

Defoliation Treatments:

Our population consisted of 600 trees from three different locations. Trees selected were of comparable size and had no signs of previous damage or diseases. Mean height of selected trees was 77.2 ± 0.61 cm, and mean stem diameter was 14.3 ± 0.13 mm. Twenty five trees were randomly assigned to each treatment at each location. Four levels of defoliation intensities (0, 25, 50 and 75%) were applied once in either spring (early June) or summer (mid August) 1988. Each tree received one of the four defoliation intensities. Defoliation was done by stripping current year's twigs by hand. Defoliation was evenly distributed over the crown starting from the base of the tree up to the apical leader that was left intact. The fresh samples were used to measure leaf area (cm^2) using leaf area meter (Table 3-1). Twigs removed were collected in paper bags, oven dried for 48 hours at 70 °C.

For all the trees, length and width of five randomly selected dominant twigs in each whorl were measured to the nearest (cm) in July 1989 and August 1990. Counting from the dominant, the fifth subdominant twig in the same branch was also measured. Number of twigs in each whorl was counted during summer 1989 and 1990 (Figure 3-1)

Table 3-1. Leaf Area (cm^2) and Oven-Dry Weight (gm) of Twigs Removed, June (Spring) and August (Summer), 1988.

Season	0%	25%	50%	75%	Average
		Defoliation Intensity			
			[1] LAI		
Spring	0.00	845.78 (206.3)	1037.30 (195.6)	1527.11 (198.5)	892.6 (98.99)
Summer	0.00	696.11 (195.1)	1591.75 (196.4)	2058.36 (195.2)	1061.5 (98.98)
Average	0.00	770.95 (141.4)	1314.52 (139.2)	1792.74 (139.7)	
			Oven Dry Weight		
Spring	0.00	12.05 (2.89)	15.41 (2.74)	22.21 (2.78)	12.98 (1.39)
Summer	0.00	18.99 (2.73)	33.32 (2.75)	45.61 (2.73)	24.13 (1.39)
Average	0.00	15.52 (1.98)	24.37 (1.95)	33.91 (1.96)	

[1] LAI: Leaf Area Index.
Standard error values are shown in parentheses.

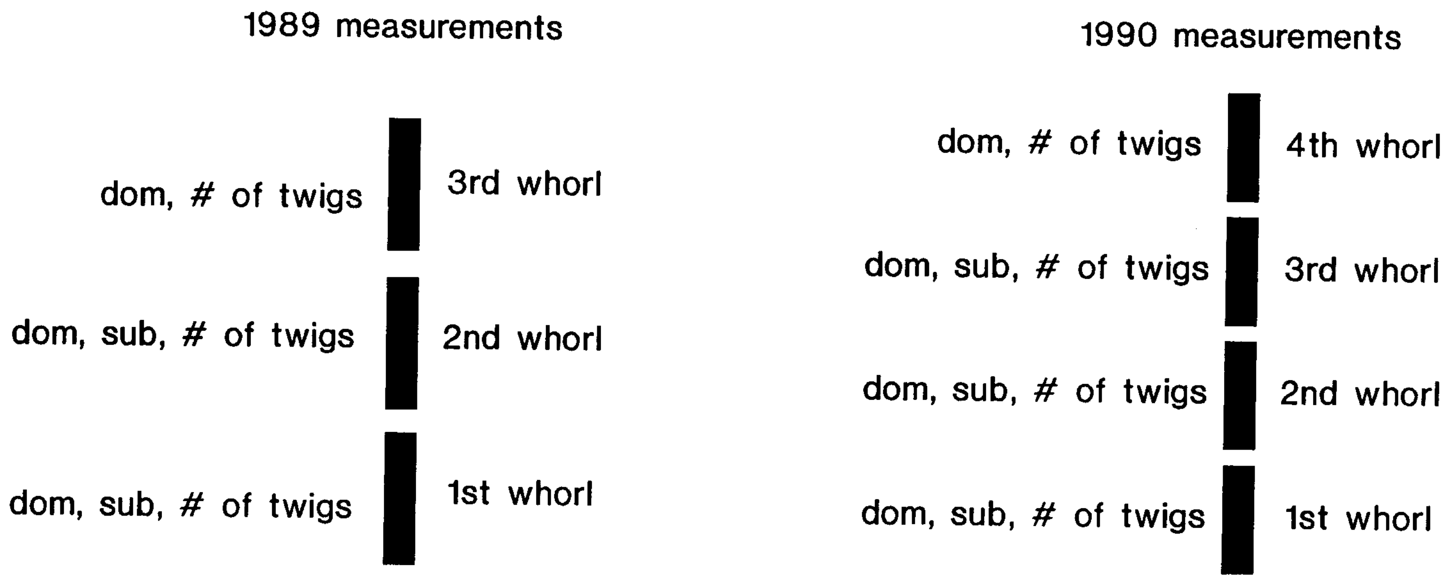


Figure 3-1. Measurements of Dominants, Subdominants, and Number of Twigs.

Plantation Management:

In an attempt to reduce competition, high intensity short duration sheep grazing was used as a silvicultural tool for vegetation management (Sharrow *et al*, 1989). The study areas were grazed in late July 1988 and early August 1989. To prevent animal damage, Big Game Repellant (BGR) was applied in July 1988 and August 1989 before sheep were introduced to the site. No tree damage due to the BGR was observed. To minimize deer damage during winter, all trees were protected in December 1988 using plastic mesh budcaps, which were removed in late April 1989. Combined sheep and deer browsing during the study period was negligible, being only 1.2 percent of terminals.

Statistical Analysis:

Collected data were analyzed as a 4 X 2 factorial in a randomized complete block design with three locations as replications (Snedecor and Cochran, 1989). Treatments (four intensities, two seasons of defoliations) were randomly assigned to two hundred trees within each block. Data were adjusted for initial tree diameter by covariance. The following model (Steel and Torrie, 1980) was used:

$$Y_{ijk} = \mu + \rho_i + \alpha_j + \tau_k + (\alpha\tau)_{jk} + \beta(X_{ijk} - \bar{X}...) + \epsilon_{ijk}$$

Where:

Y_{ijk} = dependent variable.
μ = overall mean.
ρ_i = effect of the ith block.
α_j = added effect of the jth level of season.
τ_k = added effect of the kth level of intensity.
$(\alpha\tau)_{jk}$ = added effect of the interaction between season and intensity.
β = regression coefficient.
X = independent or covariable.
ϵ_{ijk} = random error.

Means for significant differences ($P < 0.05$) were separated by Fisher's protected LSD procedure (Snedecor and Cochran, 1989). Response surfaces for significant intensity effects were developed using least squares regression procedures (Netter and Wasserman, 1989). Best fit response surfaces were selected from linear, quadratic and cubic models using stepwise linear regression in SAS (SAS Institute, 1990). Best fit models were those which had the lowest Mallow's Cp, highest R^2 and whose individual regression coefficients were all significantly different from zero ($P < 0.05$).

Results and Discussion

Responses of Dominant Twigs:

Mean area per dominant twig in all whorls decreased rapidly as defoliation intensity increased during spring. However, summer defoliation did not affect mean area per dominant twig in 1989 (Figures 3-1, 3-2 and 3-3). In 1990, with the exception of twigs in the second whorl of branches, no effects ($P > 0.05$) of defoliation intensity or season on area of dominant twigs were detected (Table 3-2). Defoliation effects upon individual twig area accrued primarily from differences in twig length. Trees defoliated to 75% in spring lost 23, 20 and 15% of their dominant twig length in the third, second and first whorls, respectively, in 1989 (Figures 3-4, 3-5 and 3-6, respectively). When defoliation was applied in summer, only the top whorl was affected and 75% defoliation reduced its length by only 7%. Season of defoliation did not affect dominant twig length in 1990 (Table 3-3). Length of twigs in third, second, and first whorls decreased by 7, 8, and 10% respectively compared to the control when 75% defoliation level was applied (Figures 3-7, 3-8, and 3-9, respectively). Defoliation intensity had less pronounced effect on dominant twig width than it did upon twig length. Defoliation applied in summer did not affect twig width in any whorl in 1989 (Table 3-4). In all whorls, twig width of spring defoliated trees was smaller than summer defoliated trees during 1989 (Table 3-4). Neither season nor intensity of defoliation affected width of twigs in any whorl in 1990 (Table 3-5). Similar results in Scots pine (*Pinus sylvestris* L.) were reported by Ericsson *et al* (1980). The differences in response between length and width of twigs are due to differences in their nature of growth. Growth of Douglas-fir twig width is determinate (Cannell *et al*, 1976). It is mostly attributable to expansion of cells that developed in the previous year (Owens, 1968). In contrast, growth of internodes (portion of stem between two successive needles) occurs largely by spring expansion of tissue initially present in the bud together with summer production of new tissue (Cannell *et al*, 1976).

Responses of Subdominant Twigs:

The uppermost whorl in 1989 (whorl 3) and in 1990 (whorl 4) contain only dominant twigs as defined for this study. Defoliation effects upon mean area per subdominant twig in second and first whorls were inconsistent. While 25% and 75% defoliation treatments differed from undefoliated control, 50% defoliation did not differ (Table 3-6). No effect of previous defoliation (in 1988) was evident in first whorls subdominant twigs in 1990. Subdominant twig area in third and second whorls continued to respond to defoliation intensity in 1990 (Figures 3-10 and 3-11, respectively). During both years, twig area was smaller ($P < 0.05$) in trees defoliated in spring than in summer.

Length of twigs was reduced by approximately 8% in each whorl following 75% defoliation in spring 1989 (Table 3-7). Similar to area, length in third and second whorls but not in first whorls continued to respond to defoliation intensity in 1990 (Figures 3-12 and 3-13, respectively). Width of subdominants in 1989 was the same for all defoliation intensities. However, spring defoliation resulted in a smaller twig width than summer defoliation (Table 3-8). Comparing the effect of treatment on the subdominant width in 1990 reveals different trends in the three whorls studied. While there was no intensity or season effect on the second whorl, the impact of season on the third and first whorl was different among intensity levels (Table 3-9).

The difference in response between dominant and subdominant twigs probably reflects differences in their source-sink relationships. The fact that defoliation treatment did not affect dominant twig area in 1990, except second whorls, suggests that dominant twigs are more competitive for photosynthate than subdominant twigs. Subdominant twigs may have lower priority for photosynthate allocation than dominant twigs. Another reason is that, photosynthate from mature leaves is distributed not only according to the size (Waring and Patrick, 1975) and requirements of different organs comprising the sinks, but also the proximity of these organs to the source leaf (Larson and Gordon, 1969). Fully grown new needles are considerably more active, photosynthetically, than older ones (Kramer and Kozlowski, 1979). Smaller amounts of photosynthate are obtained from 2 and 3-year old needles than from current year's needles (Freeland, 1952; O'Neil, 1962; Kramer and

Kozlowski, 1979). It is possible that, old and shaded needles below subdominant twigs were less capable of producing photosynthate than younger, less shaded needles near the dominant branches.

Throughout the experiment, length, width and area of dominant and subdominant twigs were smaller than or similar to ($P < 0.05$) for spring compared to summer defoliated trees. Spring defoliation was done during the period of completion of leaf expansion and before the replenishing of storage reserves. Defoliation is known to be most adverse when leaves are nearly fully expanded (Wargo, 1978). At this time all parts are growing rapidly and trees have maximum energy demands with little reserve carbohydrates. Stress at this time is known to have greater effect than it would have later in the season (Waring, 1987). It is worth-mention that the efficiency of current needles depends on their degree of maturity (O'Neil, 1962). Glucose and fructose reach their highest concentrations in August and September and lowest in May in pines (Bernard-Dagan, 1988). Current needles are initially a drain on the tree, but by mid summer their photosynthesis capacity is greater than old needles (Kulman, 1965; O'Neil, 1962). Maximum C^{14} export occurs when leaves just attain their maximum size (Larson and Gordon, 1969). Presumably, our summer defoliation allowed the trees more time to grow (from June to August) and save them better opportunity for photosynthate rebuild (longer leaf area duration) than did spring (June) defoliation.

Responses of Number of Twigs:

Number of twigs in the upper most whorls (whorl 3 in 1989 and whorl 4 in 1990) did not differ among defoliation treatments in either 1989 or 1990. Number of twigs in second and third in 1989 whorls decreased linearly as defoliation level increased (Figures 3-14 and 3-15). However, with the exception of second whorls, intensity of defoliation showed no effect on number of twigs in 1990 (Table 3-10). Summer defoliation, in general, was less detrimental to twig number than was spring defoliation (Table 3-10) Similar number of 1990 twigs produced per 1989 twig for all defoliation treatments suggest that the residual effect in whorl 2 reflects fewer 1989 twigs produced as defoliation increased rather than a direct defoliation effect on 1990 tree growth.

Figure 3-2. Response surface relating defoliation intensity (%) to average area of dominant twigs (cm^2) in the third whorl (top), July 1989.

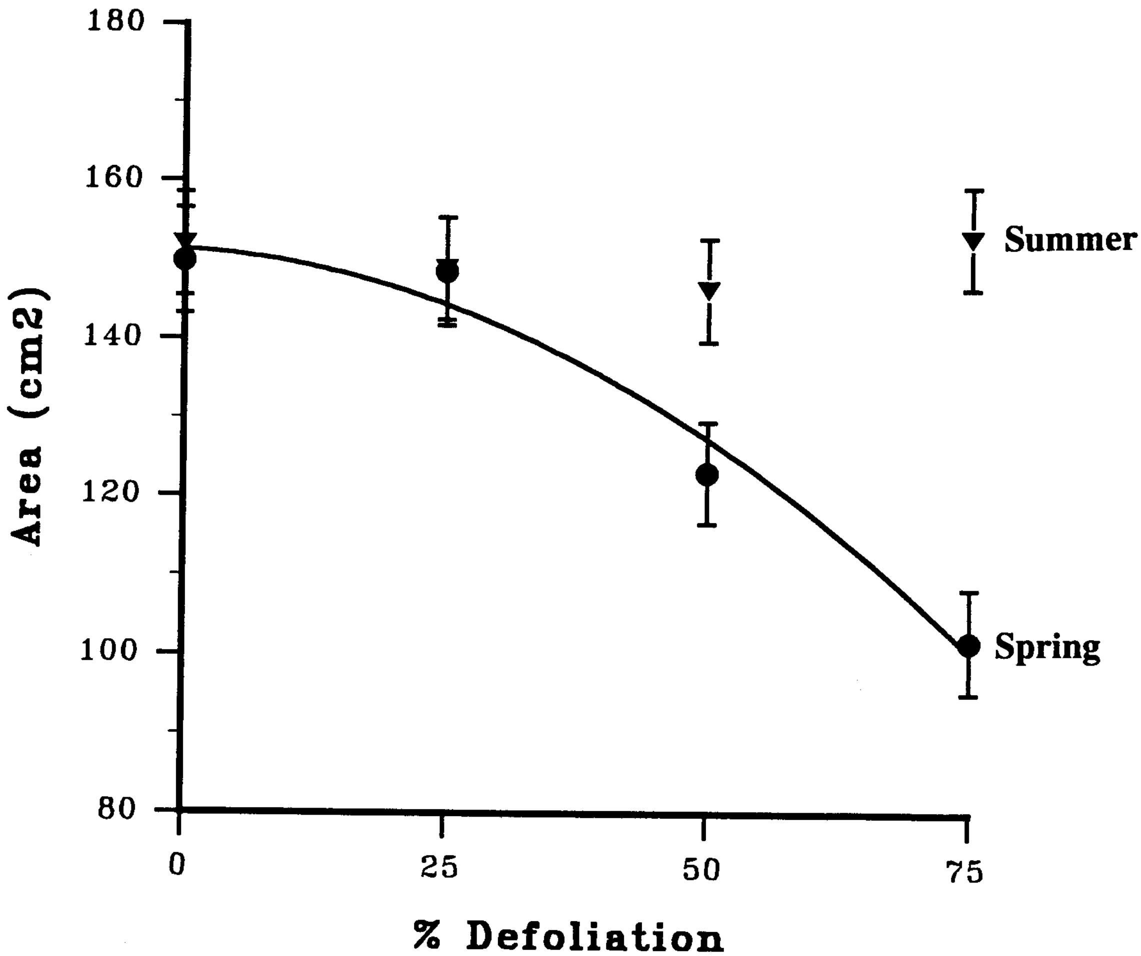
Spring:

Mean Area = 147.0 - 0.0081 %Intensity^2

R^2 = 0.89 Cp = 2.0

Summer:

No Intensity Effects were Detected



180
160
140
120
100
80
Area (cm2)
0
25
50
75
% Defoliation
Summer
Spring

Figure 3-2.

Figure 3-3. Response surface relating defoliation intensity (%) to average area of dominant twigs (cm^2) in the second whorl (middle), July 1989.

Spring:

Mean Area = 130.7 - 0.0055 %Intensity^2

R^2 = 0.82 Cp = 2.0

Summer:

No Intensity Effects were Detected

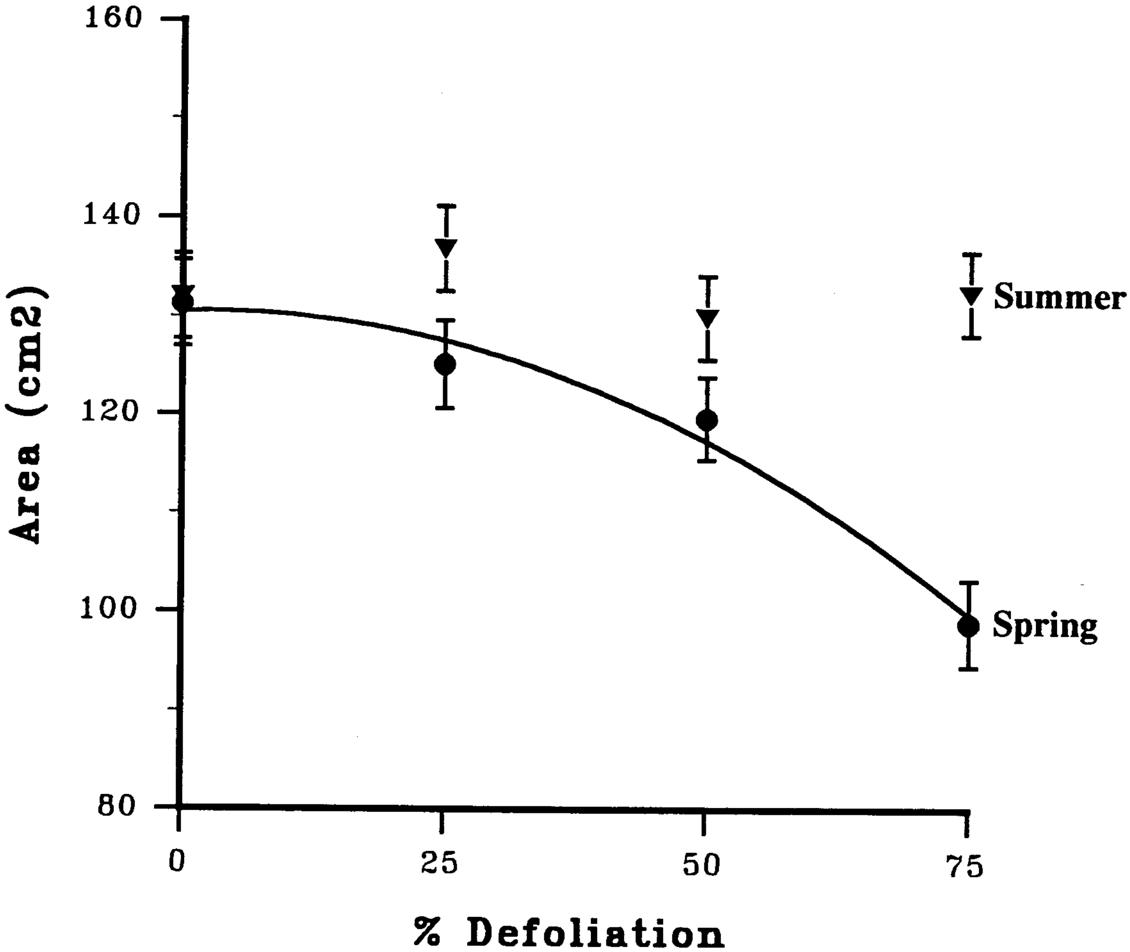

160
140
120
100
80
Area (cm2)
0
25
50
75
% Defoliation
Summer
Spring

Figure 3-3.

Figure 3-4. Response surface relating defoliation intensity (%) to average area of dominant twigs (cm^2) in the first whorl (bottom), July 1989.

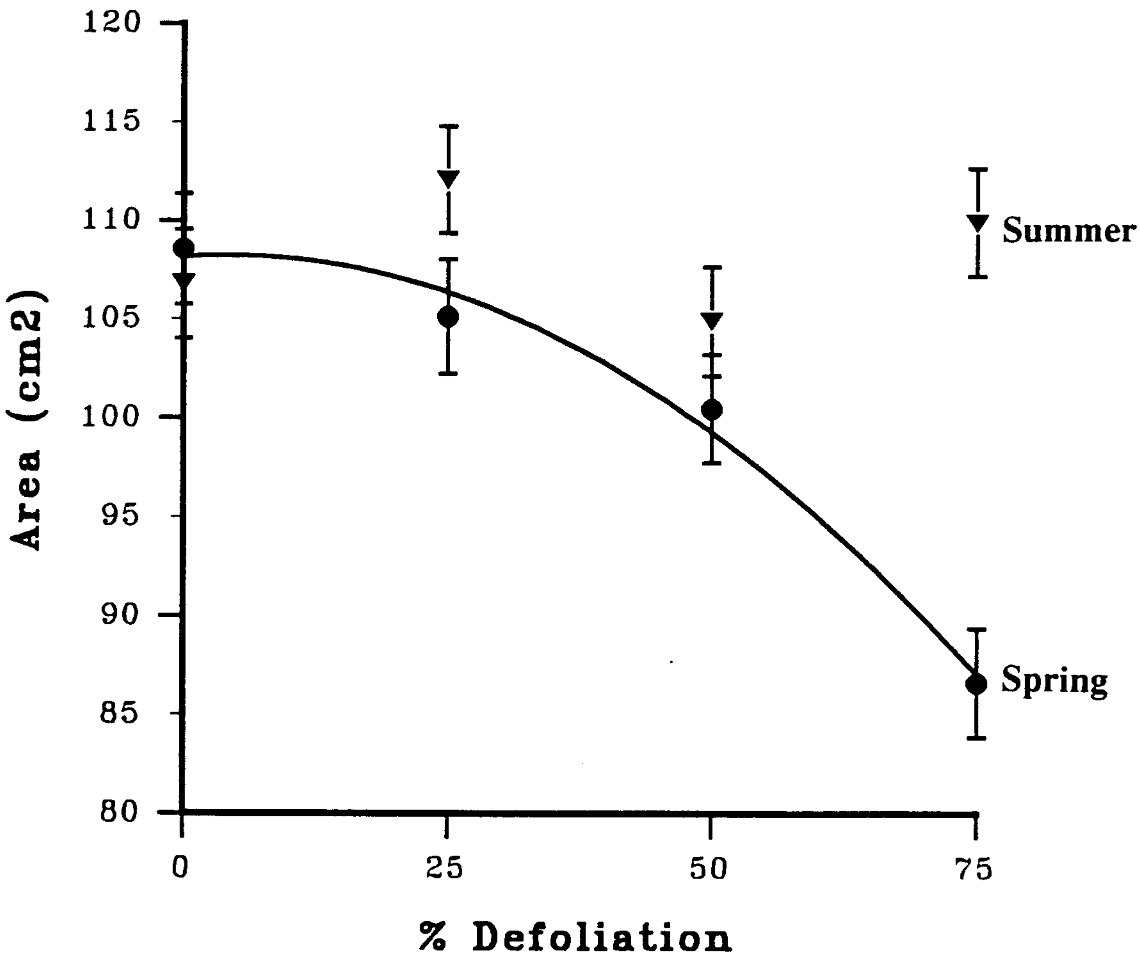
Spring:

Mean Area = 107.6 - 0.0035 %Intensity^2

R^2 = 0.90 Cp = 2.0

Summer:

No Intensity Effects were Detected



120
115
110
105
100
95
90
85
80
Area (cm2)
0
25
50
75
% Defoliation
Summer
Spring

Figure 3-4.

Figure 3-5. Response surface relating defoliation intensity (%) to average length of dominant twigs (cm) in the third whorl (top), July 1989.

Spring:

Mean Length = 27.4 - 0.0011 %Intensity²

$$R^2 = 0.88 \quad Cp = 2.6$$

Summer:

Mean Length = 28.2 - 0.0301 %Intensity

$$R^2 = 0.98 \quad Cp = 3.5$$

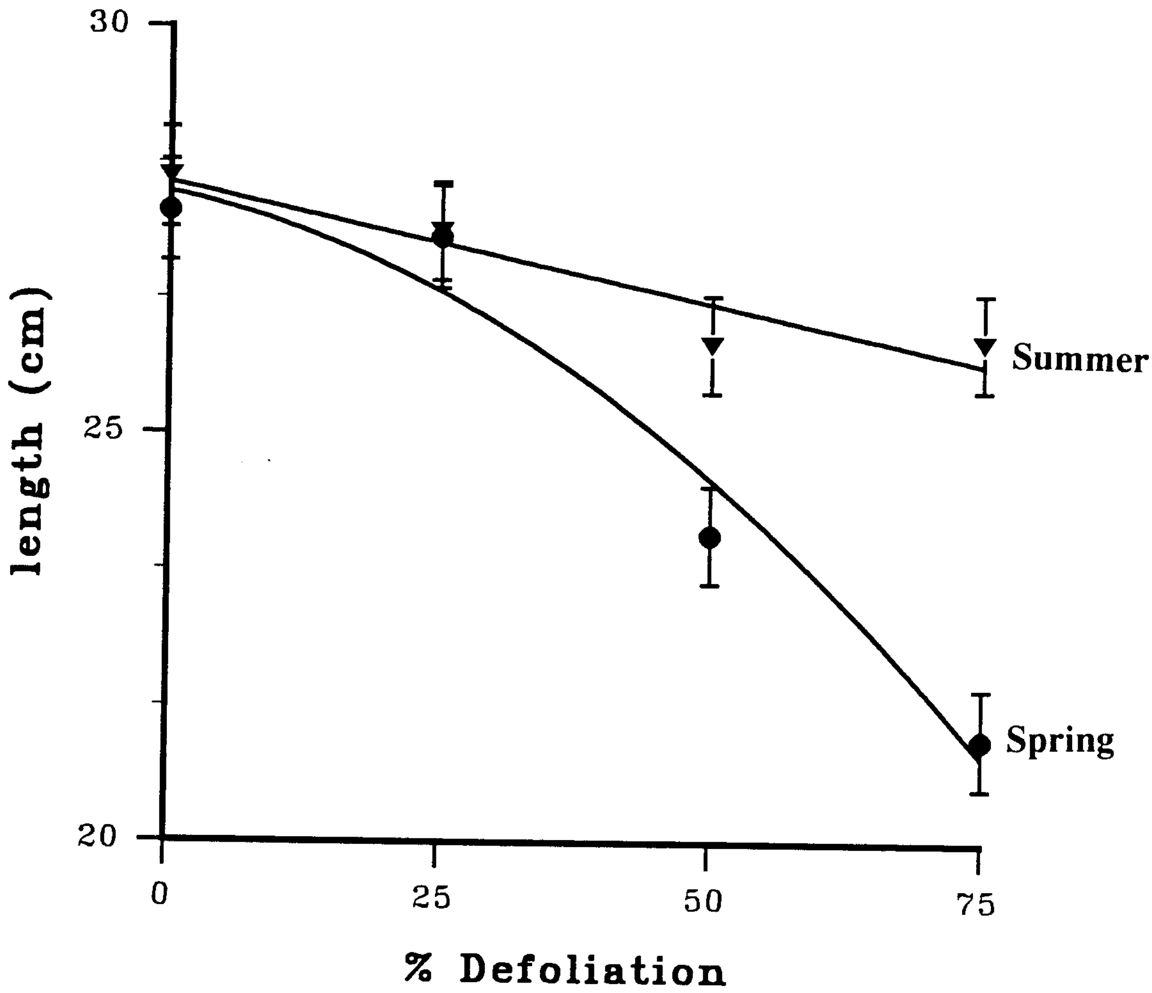


Figure 3-5.

Figure 3-6. Response surface relating defoliation intensity (%) to average length of dominant twigs (cm) in the second whorl (middle), July 1989.

Spring:

Mean Length = 24.0 - 0.0008 %Intensity^2

R^2 = 0.85 Cp = 1.97

Summer:

No Intensity Effects were Detected

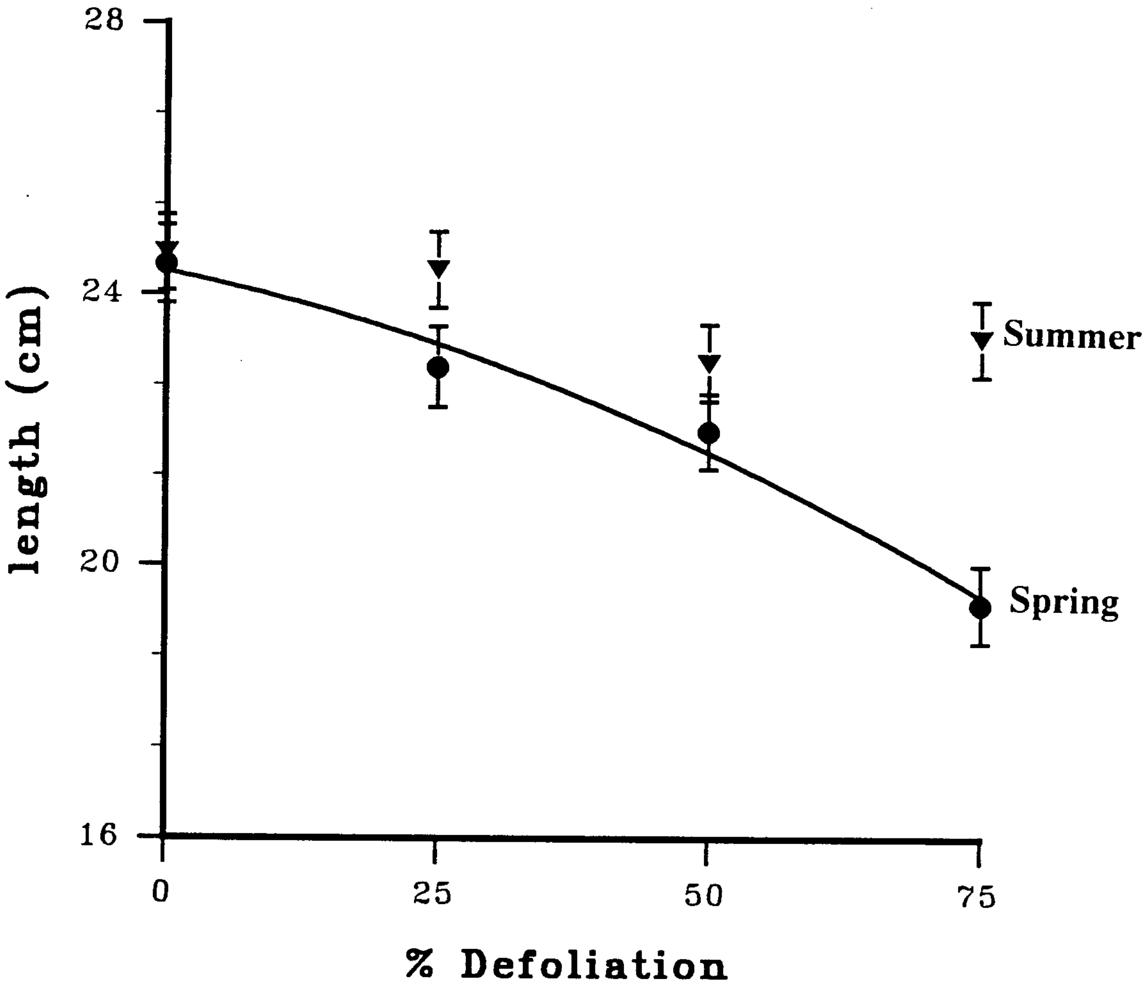


Figure 3-6.

Figure 3-7. Response surface relating defoliation intensity (%) to average length of dominant twigs (cm) in the first whorl (bottom), July 1989.

Spring:

Mean Length = 17.7 - 0.0005 %Intensity^2

R^2 = 0.88 Cp = 1.3

Summer:

No Intensity Effects were Detected

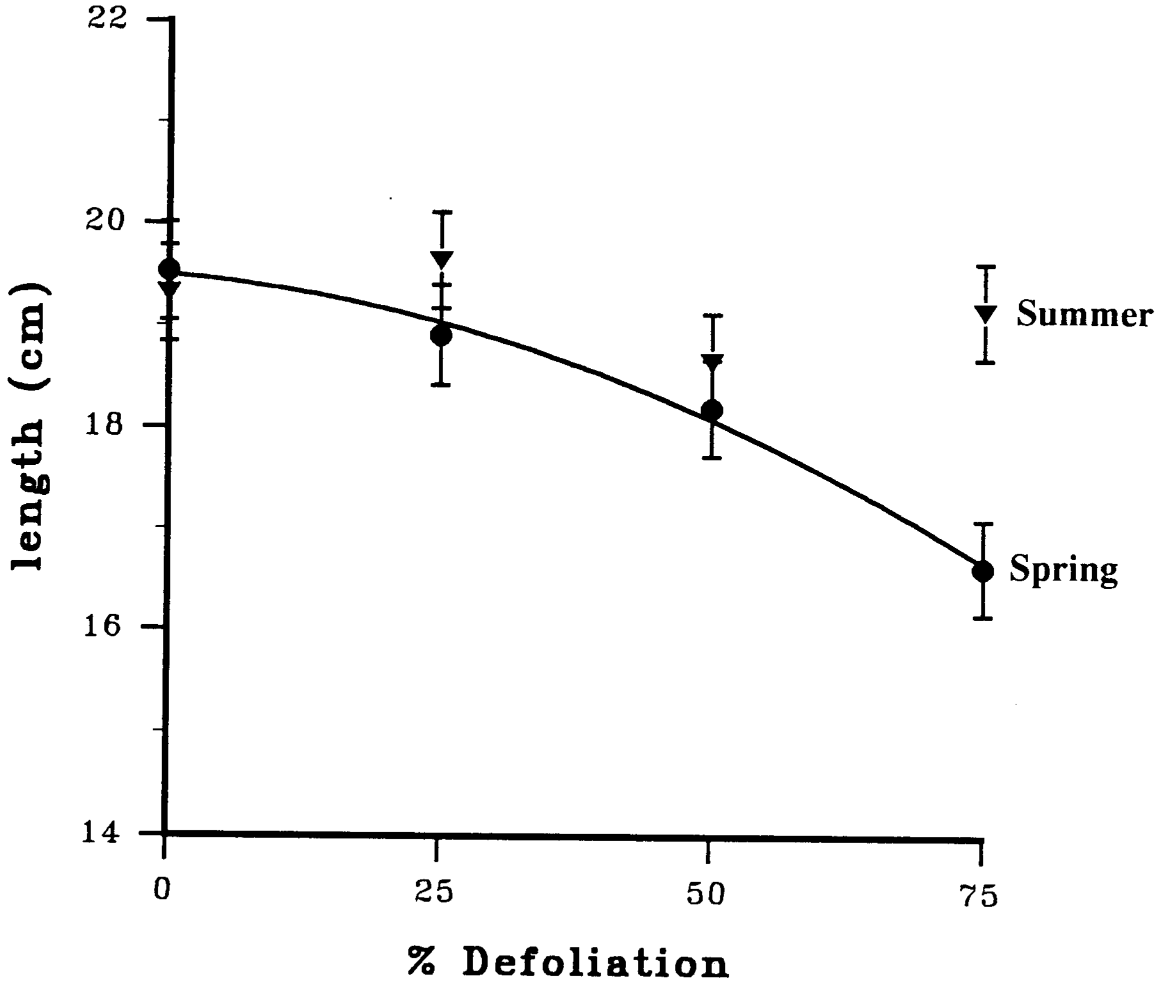


Figure 3-7.

Figure 3-8. Response surface relating defoliation intensity (%) to average length of dominant twigs (cm) in the third whorl (top), August 1990.

Mean Length = 40.5 - 0.046 %Intensity
R^2 = 0.91 Cp = 1.9

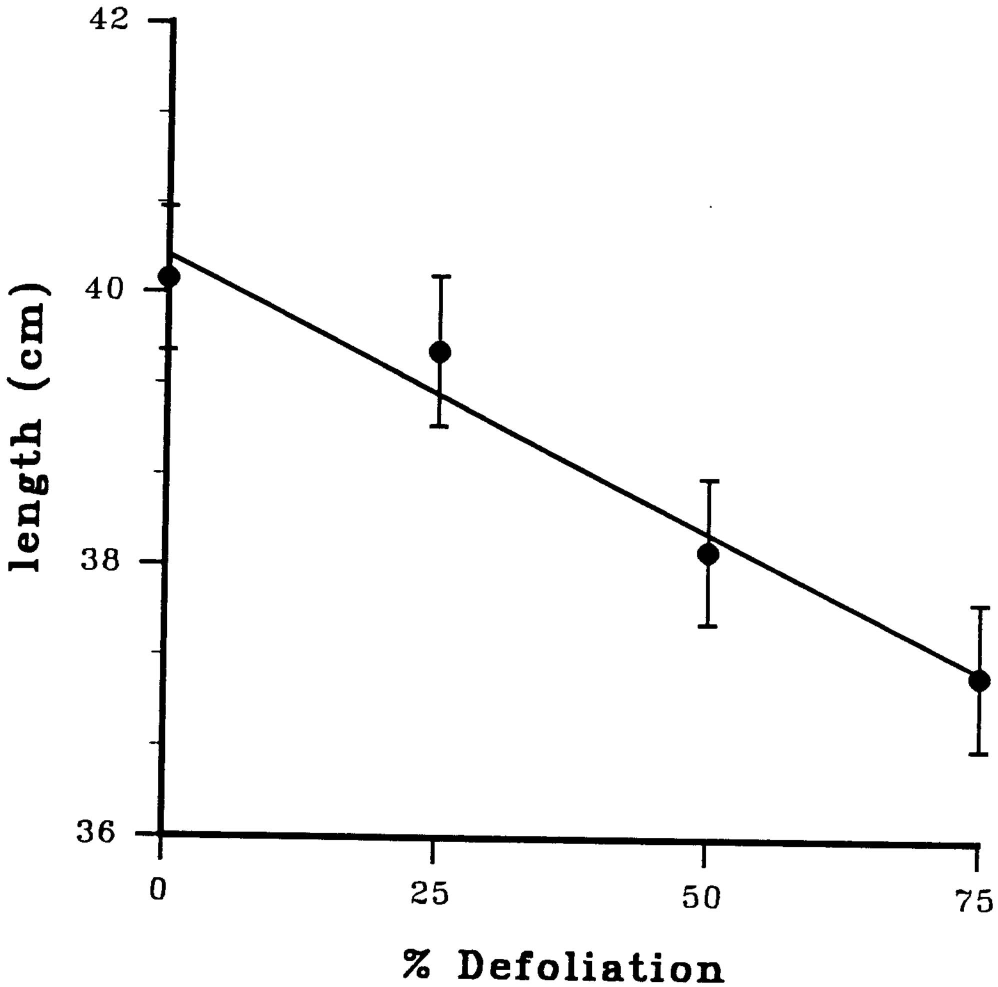


Figure 3-8.

Figure 3-9. Response surface relating defoliation intensity (%) to average length of dominant twigs (cm) in the second whorl (middle), August 1990.

Mean Length = 32.5 - 0.0006 %Intensity^2
R^2 = 0.83 Cp = 1.5

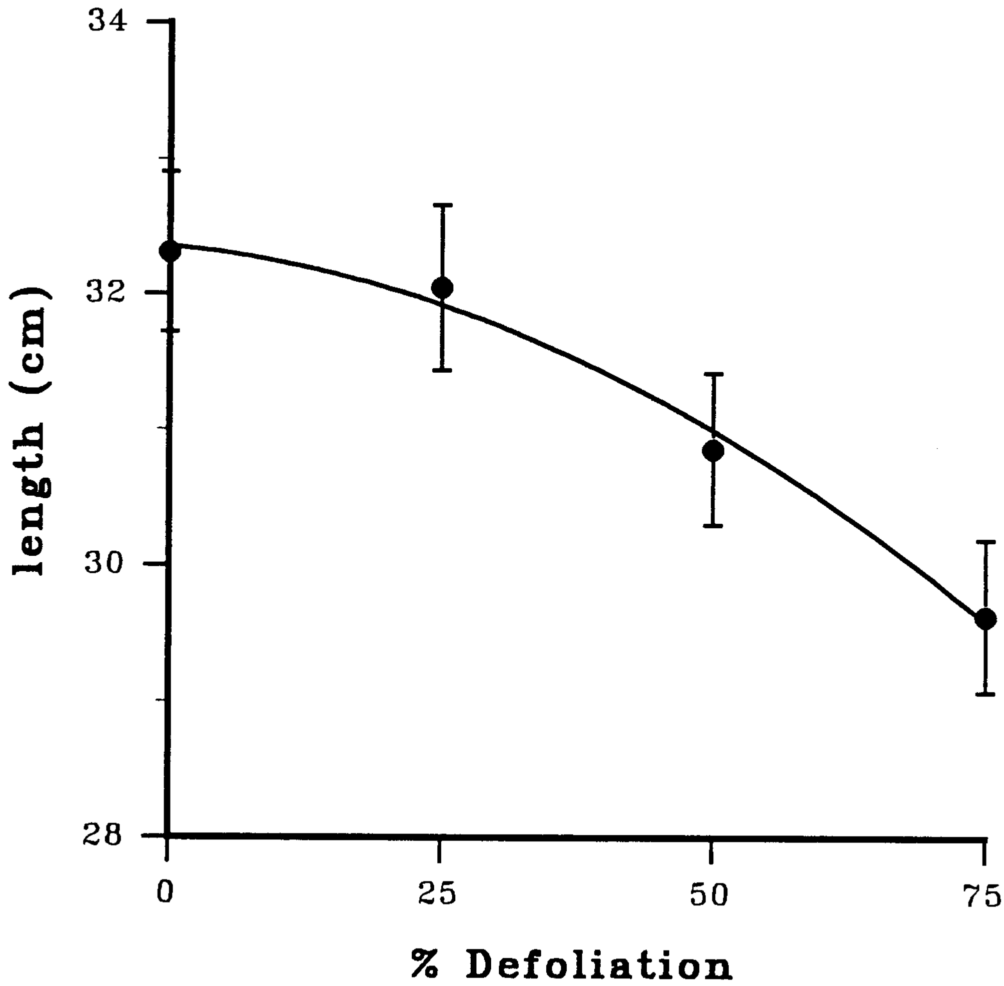


Figure 3-9.

Figure 3-10. Response surface relating defoliation intensity (%) to average length of dominant twigs (cm) in the first whorl (bottom), August 1990.

Mean Length = 25.2 - 0.0005 %Intensity^2
R^2 = 0.87 Cp = 2.2

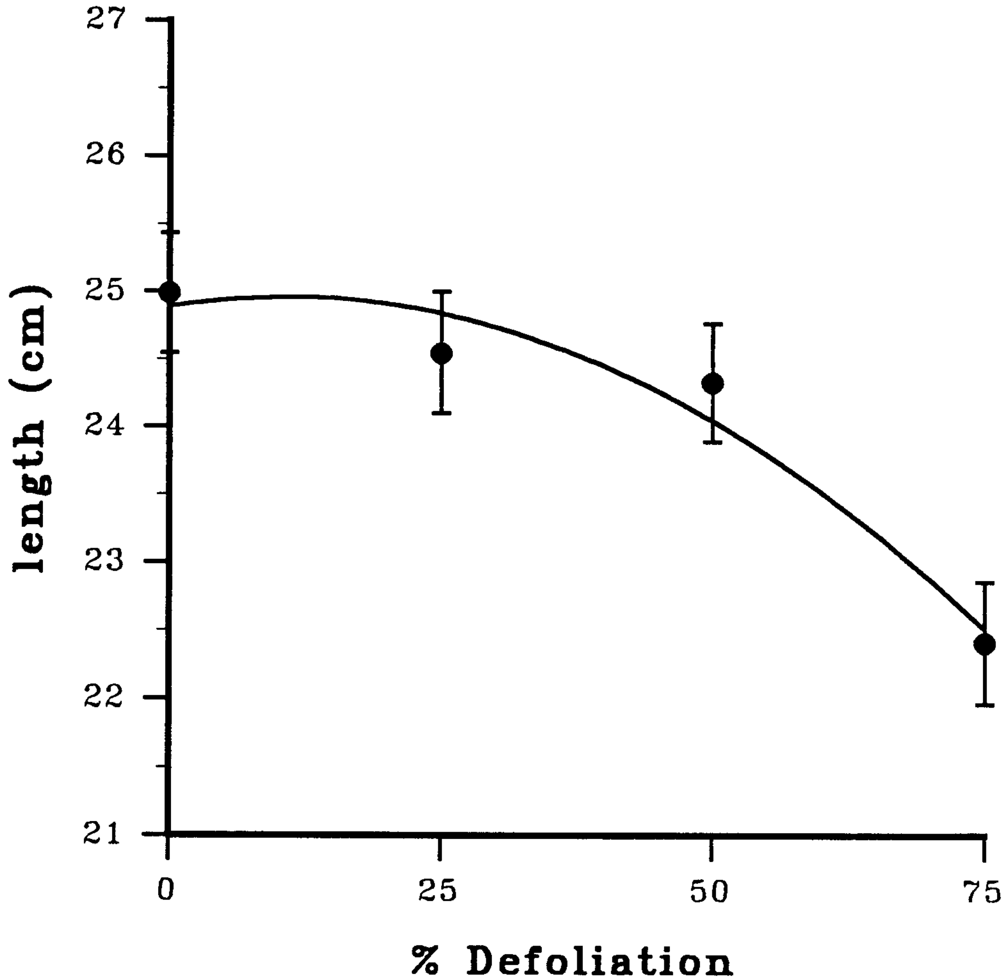


Figure 3-10.

Figure 3-11. Response surface relating defoliation intensity (%) to average area of subdominant twigs (cm^2) in the third whorl (top), August 1990.

Spring:
Mean Area = 87.9 - 0.0034 Intensity^2
R^2 = 0.84 Cp = 1.4
Summer:
Mean Area = 85.8 - 0.0012 Intensity^2
R^2 = 0.96 Cp = 5.4

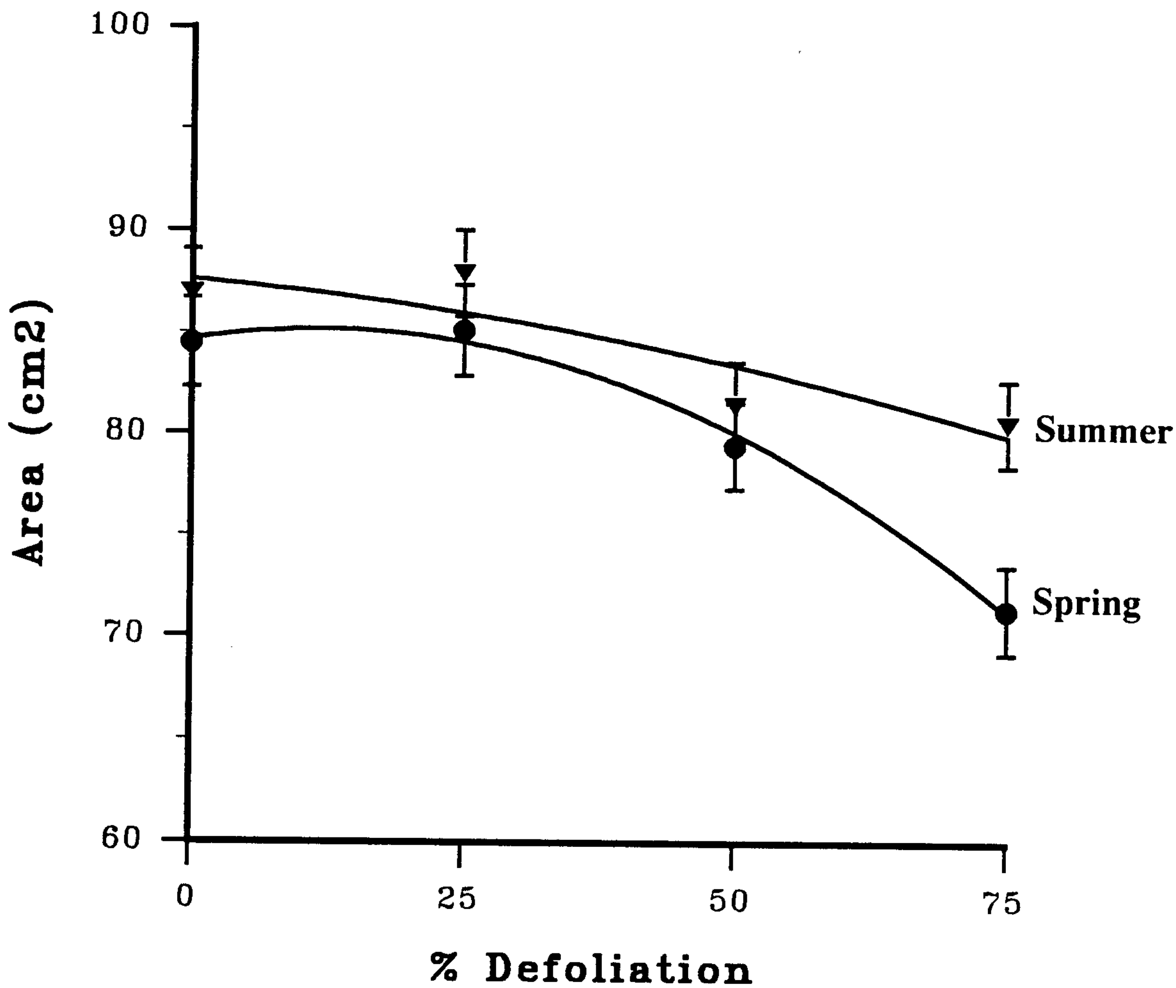


Figure 3-11.

Figure 3-12. Response surface relating defoliation intensity (%) to average area of subdominant twigs (cm^2) in the second whorl (middle), August 1990.

Spring:

Mean Area = 66.7 - 0.0025 Intensity^2

R^2 = 0.84 Cp = 1.4

Summer:

No Intensity Effects were Detected

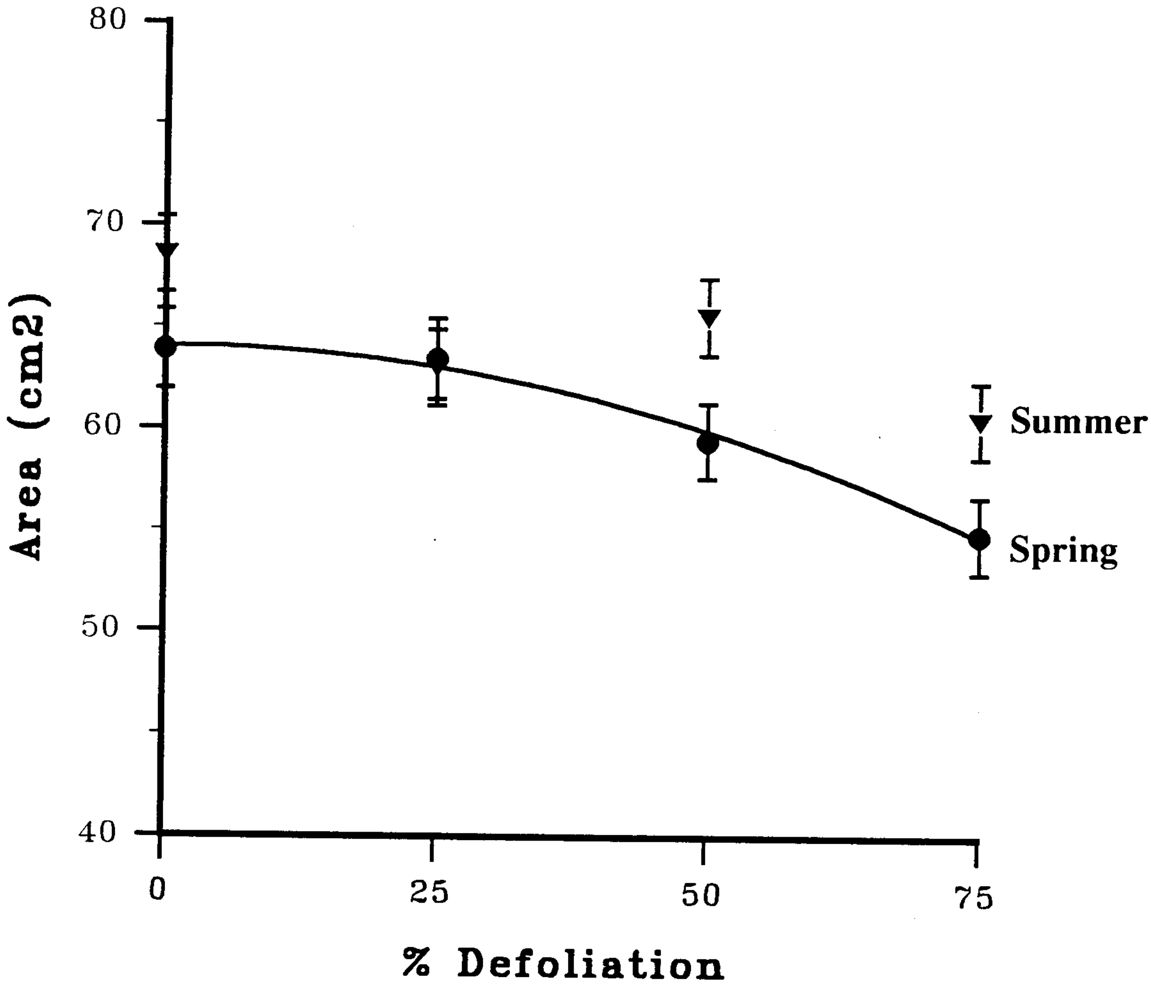


Figure 3-12.

Figure 3-13. Response surface relating defoliation intensity (%) to average length of subdominant twigs (cm) in the third whorl (bottom), August 1990.

Spring:

Mean Length = 16.3 - 0.0005 Intensity^2

R^2 = 0.79 Cp = 1.5

Summer:

Mean Length = 16.1 - 0.0002 Intensity^2

R^2 = 0.94 Cp = 1.7

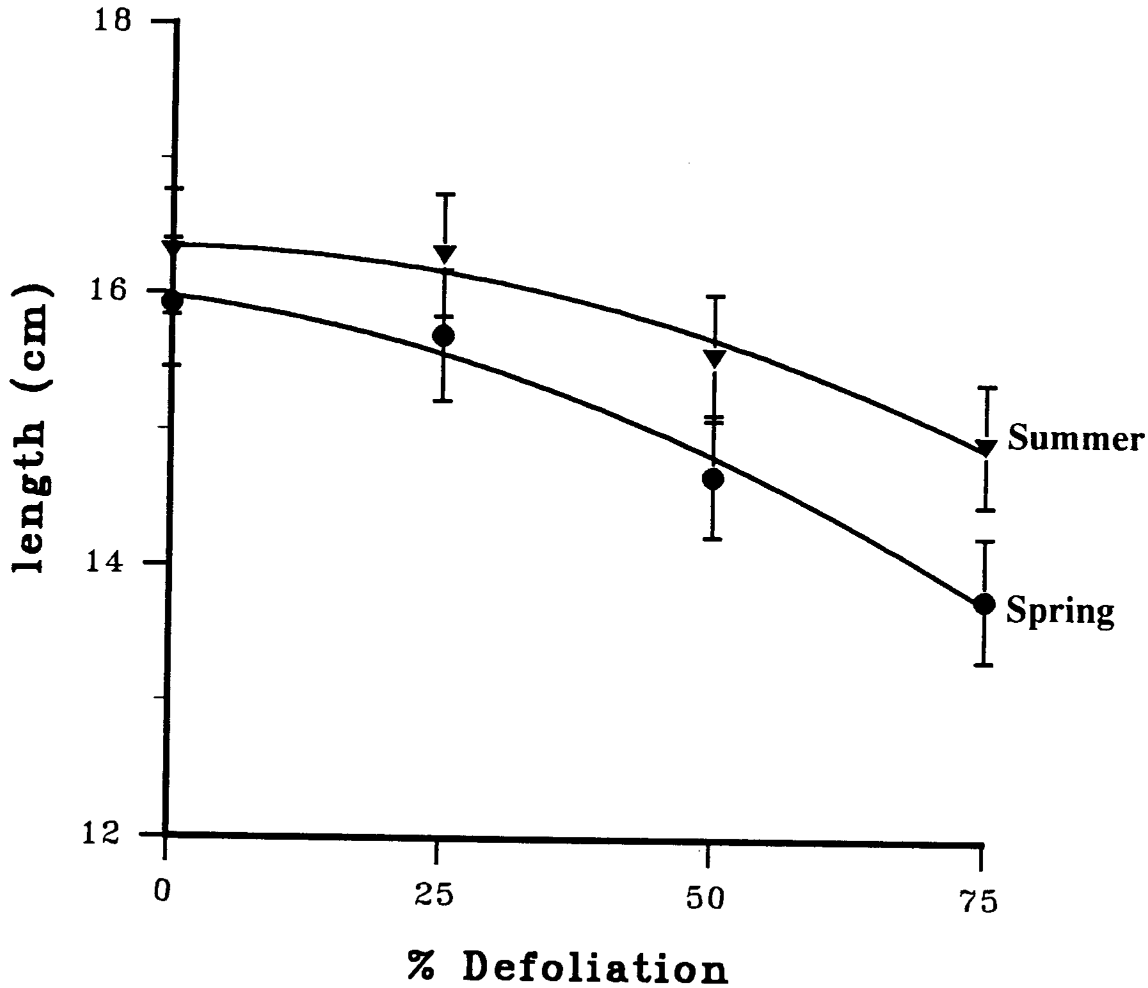


Figure 3-13.

Figure 3-14. Response surface relating defoliation intensity (%) to average length of subdominant twigs (cm) in the second whorl (middle), August 1990.

Spring:

Mean Length = 12.9 - 0.0003 Intensity^2

R^2 = 0.83 Cp = 1.9

Summer:

No Intensity Effects were Detected

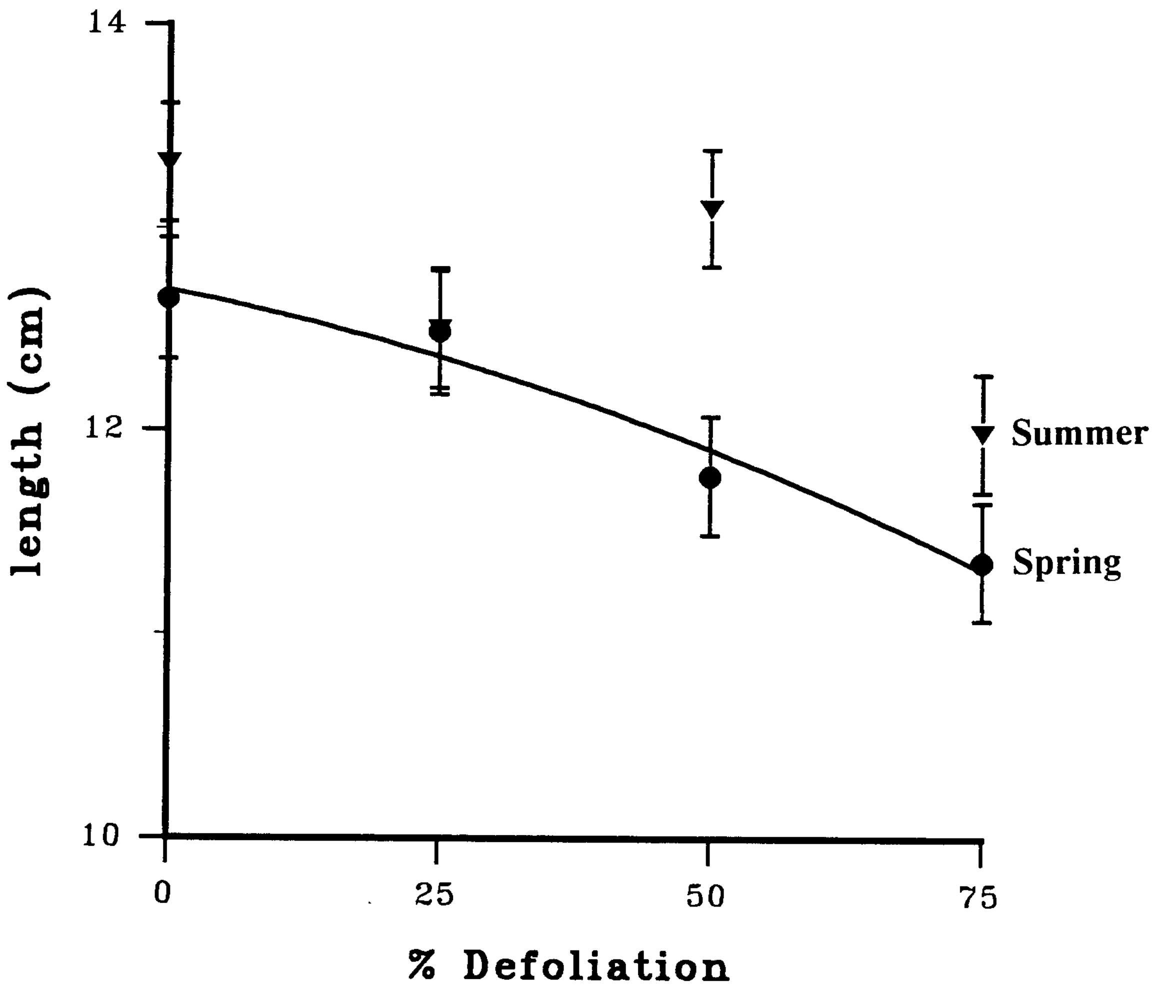


Figure 3-14.

Figure 3-15. Response surface relating defoliation intensity (%) to number of twigs in the second whorl (middle), July 1989.

Number of Twigs = 115.0 - 0.5402 %Intensity

R^2 = 0.77 Cp = 4.7

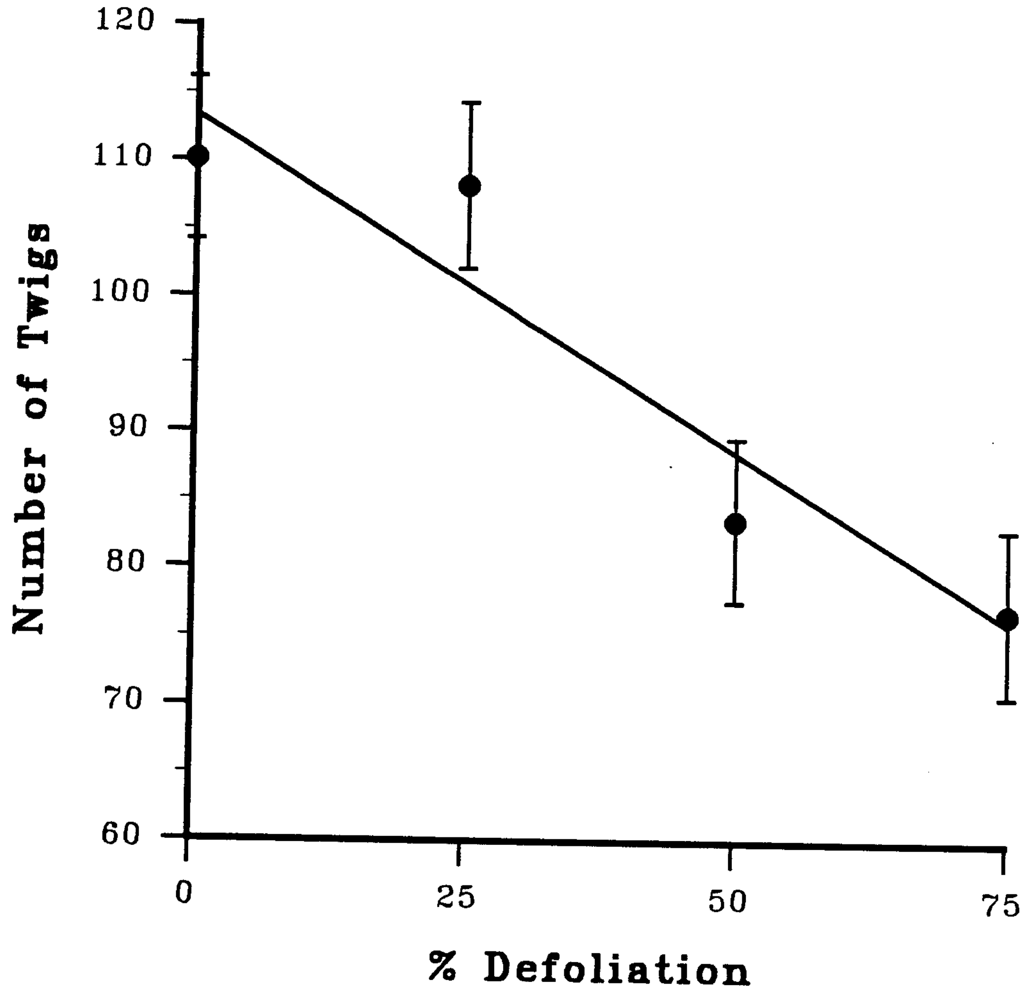


Figure 3-15.

Figure 3-16. Response surface relating defoliation intensity (%) to number of twigs in the first whorl (bottom), July 1989.

Number of Twigs = 263.9 - 0.8543 %Intensity

$R^2 = 0.74$ **Cp = 3.0**

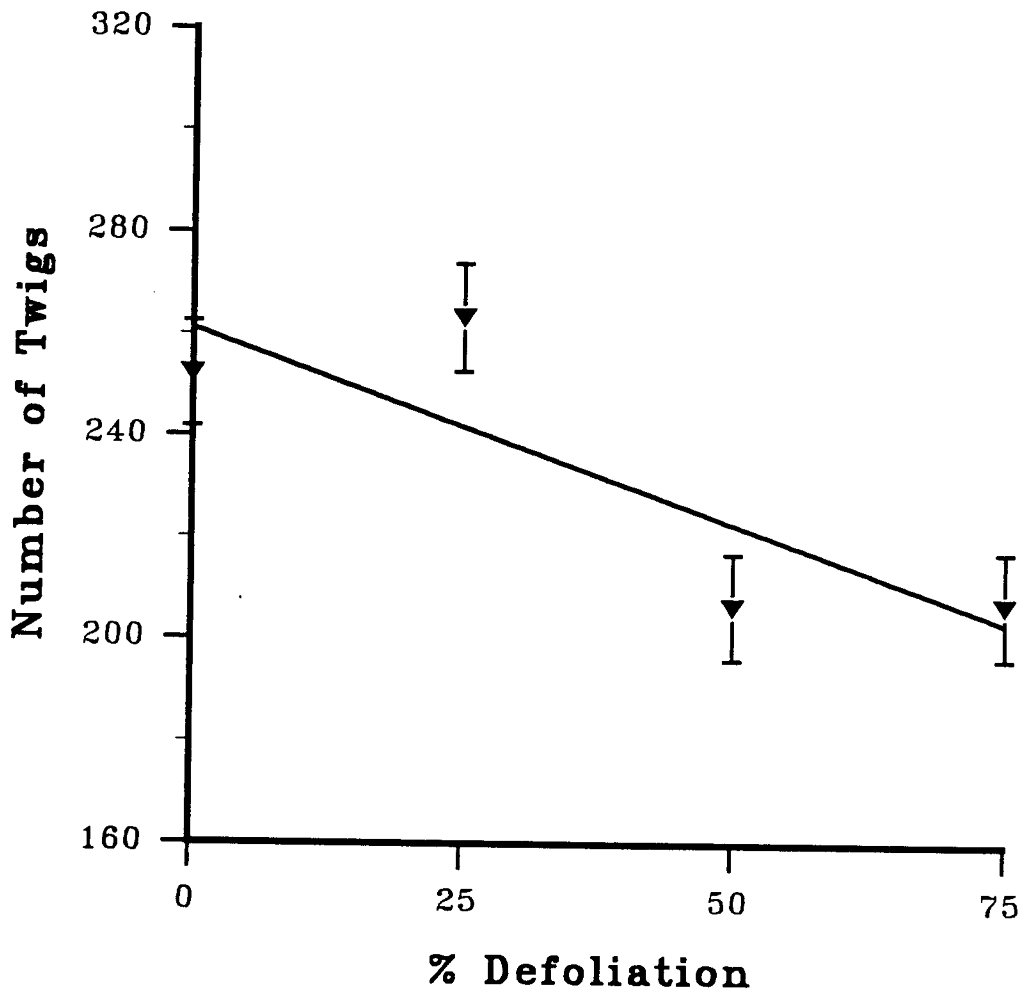


Figure 3-16.

Figure 3-17. Response surface relating defoliation intensity (%) to number of twigs in the second whorl (middle), July 1990.

Number of Twigs = 285.7 - 1.6440 %Intensity

R^2 = 0.63 Cp = 3.0

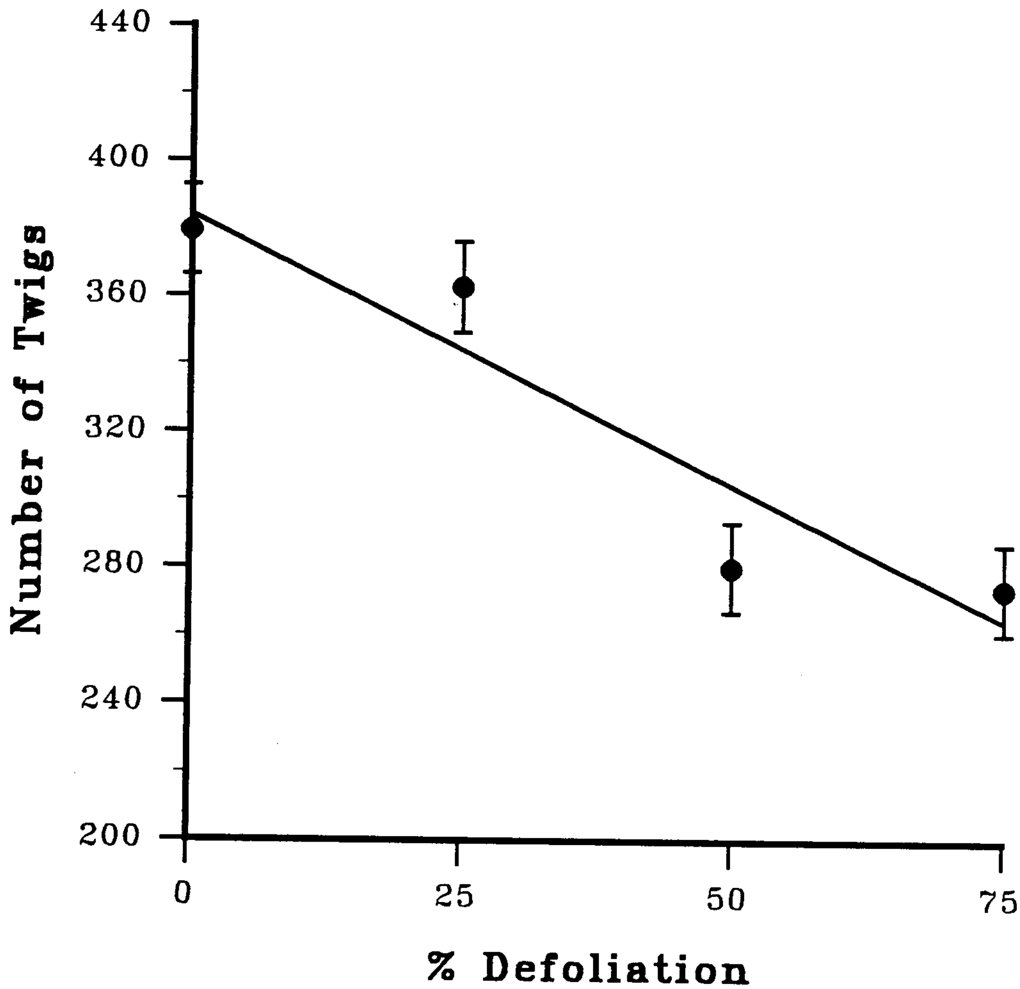

440
400
360
320
280
240
200
Number of Twigs
0
25
50
75
% Defoliation

Figure 3-17.

Table 3-2. Effects of Defoliation Intensity and Season on Mean Area (cm^2) of Douglas-fir Dominant Twigs August, 1990.

	Defoliation Intensity				
Season	0%	25%	50%	75%	Average
			[1] *Whorl 4*		
Spring	218.3 (8.5)a	226.8 (8.7)a	220.7 (8.2)a	212.9 (8.4)a	219.7 (4.2)a
Summer	233.0 (8.3)a	218.3 (8.2)a	217.4 (8.3)a	220.6 (8.2)a	222.3 (4.2)a
Average	225.6 (5.8)a	222.5 (6.0)a	219.0 (5.9)a	216.7 (5.9)a	
			Whorl 3		
Spring	237.2 (7.7)a	248.2 (7.8)a	237.6 (7.4)a	220.1 (7.6)a	235.8 (3.8)a
Summer	248.5 (7.5)a	231.2 (7.4)a	232.2 (7.5)a	233.2 (7.4)a	236.3 (3.8)a
Average	242.8 (5.3)a	239.7 (5.4)a	234.9 (5.3)a	226.7 (5.3)a	
			Whorl 2		
Spring	180.5 (6.2)a	201.3 (6.3)b	190.8 (6.0)ab	174.4 (6.1)a	186.8 (3.0)a
Summer	202.8 (6.1)a	185.9 (6.0)ab	183.0 (6.0)b	180.4 (6.0)b	188.0 (3.0)a
Average	191.7 (4.2)a	193.6 (4.3)a	186.9 (4.3)ab	177.4 (4.3)b	
			Whorl 1		
Spring	139.7 (13.1)a	151.9 (13.4)a	141.7 (12.7)a	150.0 (12.9)a	145.8 (6.4)a
Summer	175.5 (12.8)a	137.7 (12.7)a	138.8 (12.8)a	129.5 (12.7)a	145.4 (6.4)a
Average	157.6 (9.0)a	144.8 (9.2)a	140.3 (9.0)a	139.7 (9.1)a	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha = 0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-3. Effects of Defoliation Intensity and Season on Average Length (cm) of Douglas-fir Dominant Twigs August, 1990.

Season	Defoliation Intensity 0%	25%	50%	75%	Average
			[1] Whorl 4		
Spring	40.56 (1.07)a	40.77 (1.09)a	39.89 (1.03)a	38.93 (1.05)a	40.04 (0.52)a
Summer	41.74 (1.04)a	39.68 (1.03)a	39.70 (1.04)a	39.40 (1.03)a	40.13 (0.52)a
Average	41.15 (0.73)a	40.22 (0.75)a	39.79 (0.74)a	39.16 (0.74)a	
			Whorl 3		
Spring	39.15 (0.78)ab	40.76 (0.80)a	37.82 (0.76)bc	36.79 (0.77)c	38.63 (0.38)a
Summer	41.07 (0.76)a	38.40 (0.75)b	38.43 (0.76)b	37.64 (0.75)b	38.88 (0.38)a
Average	40.11 (0.53)a	39.58 (0.55)ab	38.12 (0.54)bc	37.21 (0.54)c	
			Whorl 2		
Spring	30.63 (0.86)ab	33.05 (0.88)a	30.91 (0.84)ab	29.63 (0.85)b	31.06 (0.42)a
Summer	33.98 (0.85)a	31.05 (0.84)b	30.80 (0.84)b	29.63 (0.84)b	31.36 (0.42)a
Average	32.31 (0.59)a	32.05 (0.61)a	30.86 (0.60)ab	29.63 (0.60)b	
			Whorl 1		
Spring	24.28 (0.64)ab	25.13 (0.66)a	24.08 (0.62)ab	22.48 (0.63)b	23.99 (0.32)a
Summer	25.71 (0.63)a	23.97 (0.63)ab	24.58 (0.63)a	22.35 (0.62)b	24.15 (0.32)a
Average	24.99 (0.44)a	24.55 (0.45)a	24.33 (0.44)a	22.42 (0.45)b	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha=0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-4. Effects of Defoliation Intensity and Season on Average Width (cm) of Douglas-fir Dominant Twigs July, 1989.

Season	Defoliation Intensity 0%	25%	50%	75%	Average
			[(1)] Whorl 3		
Spring	5.39 (0.20)a	5.41 (0.21)a	5.18 (0.20)ab	4.77 (0.20)b	5.19 (0.10)a
Summer	5.38 (0.20)a	5.40 (0.20)a	5.54 (0.20)a	5.87 (0.20)a	5.55 (0.10)b
Average	5.39 (0.14)a	5.41 (0.14)a	5.36 (0.14)a	5.32 (0.14)a	
			Whorl 2		
Spring	5.37 (0.12)ab	5.43 (0.12)a	5.44 (0.11)a	5.06 (0.12)b	5.32 (0.06)a
Summer	5.36 (0.12)a	5.58 (0.11)a	5.66 (0.11)a	5.64 (0.11)a	5.56 (0.06)b
Average	5.36 (0.08)a	5.51 (0.08)a	5.55 (0.08)a	5.35 (0.08)a	
			Whorl 1		
Spring	5.55 (0.08)a	5.55 (0.08)a	5.52 (0.08)a	5.21 (0.08)b	5.46 (0.04)a
Summer	5.52 (0.08)a	5.69 (0.08)a	5.58 (0.08)a	5.71 (0.08)a	5.63 (0.04)b
Average	5.54 (0.05)a	5.62 (0.06)a	5.55 (0.05)a	5.46 (0.06)a	

[(1)] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha=0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-5. Effects of Defoliation Intensity and Season on Average Width (cm) of Douglas-fir Dominant Twigs August, 1990.

	Defoliation Intensity				
Season	0%	25%	50%	75%	Average
			[1] *Whorl 4*		
Spring	5.37 (0.13)a	5.56 (0.13)a	5.53 (0.13)a	5.45 (0.13)a	5.48 (0.06)a
Summer	5.56 (0.13)a	5.51 (0.13)a	5.49 (0.13)a	5.56 (0.13)a	5.53 (0.06)a
Average	5.46 (0.09)a	5.53 (0.09)a	5.51 (0.09)a	5.51 (0.09)a	
			Whorl 3		
Spring	6.07 (0.12)a	6.07 (0.12)a	6.29 (0.11)a	5.95 (0.12)a	6.09 (0.06)a
Summer	6.05 (0.12)a	6.03 (0.11)a	6.05 (0.12)a	6.20 (0.11)a	6.08 (0.06)a
Average	6.06 (0.08)a	6.05 (0.08)a	6.17 (0.08)a	6.07 (0.08)a	
			Whorl 2		
Spring	5.89 (0.13)a	6.07 (0.13)a	6.17 (0.12)a	5.85 (0.12)a	6.00 (0.06)a
Summer	5.95 (0.12)a	6.00 (0.12)b	5.94 (0.12)a	6.06 (0.12)a	5.99 (0.06)a
Average	5.92 (0.09)a	6.03 (0.09)a	6.06 (0.09)a	6.00 (0.09)a	
			Whorl 1		
Spring	5.76 (0.47)a	6.03 (0.48)a	5.88 (0.45)a	6.45 (0.46)a	6.03 (0.23)a
Summer	6.73 (0.46)a	5.75 (0.45)a	5.63 (0.45)a	5.77 (0.45)a	5.97 (0.23)a
Average	6.25 (0.32)a	5.89 (0.33)a	5.76 (0.32)a	6.10 (0.32)a	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha=0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-6. Effects of Defoliation Intensity and Season on Mean Area (cm^2) of Douglas-fir Subdominant Twigs July, 1989.

	Defoliation Intensity				
Season	0%	25%	50%	75%	Average
	[1] Whorl 2				
Spring	45.4 (1.3)a	44.7 (1.3)ab	46.0 (1.2)a	41.2 (1.3)b	44.3 (0.6)a
Summer	47.2 (1.2)a	50.7 (1.2)a	49.0 (1.2)a	48.3 (1.2)a	48.8 (0.6)b
Average	46.3 (0.9)a	47.7 (0.9)a	47.5 (0.9)a	44.8 (0.9)a	
	Whorl 1				
Spring	42.8 (1.2)a	40.4 (1.2)ab	41.0 (1.2)ab	37.5 (1.2)b	40.4 (0.6)a
Summer	42.1 (1.2)a	42.0 (1.2)a	45.9 (1.2)b	46.2 (1.2)b	44.1 (0.6)b
Average	42.4 (0.8)a	41.2 (0.8)a	43.5 (0.8)a	41.8 (0.8)a	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha=0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-7. Effects of Defoliation Intensity and Season on Average Length of Douglas-fir Subdominant Twigs July, 1989.

	Defoliation Intensity				
Season	0%	25%	50%	75%	Average
	[1] Whorl 2				
Spring	10.23 (0.20)a	9.84 (0.21)ab	9.73 (0.20)ab	9.39 (0.20)b	9.80 (0.10)a
Summer	10.24 (0.20)a	10.66 (0.20)a	10.33 (0.20)a	10.19 (0.20)a	10.36 (0.10)b
Average	10.23 (0.14)a	10.25 (0.14)a	10.03 (0.14)a	9.79 (0.14)a	
	Whorl 1				
Spring	9.44 (0.18)a	9.04 (0.19)ab	9.25 (0.18)ab	8.76 (0.18)b	9.12 (0.09)a
Summer	9.43 (0.18)a	9.35 (0.18)a	9.68 (0.18)a	9.68 (0.18)a	9.54 (0.09)b
Average	9.44 (0.13)a	9.20 (0.13)a	9.46 (0.13)a	9.22 (0.13)a	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha=0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-8. Effects of Defoliation Intensity and Season on Average Width of Douglas-fir Subdominant Twigs July, 1989.

Season	Defoliation Intensity 0%	25%	50%	75%	Average
[1] Whorl 2					
Spring	4.44 (0.08)a	4.53 (0.09)ab	4.74 (0.08)b	4.38 (0.08)a	4.52 (0.04)a
Summer	4.61 (0.08)a	4.76 (0.08)a	4.74 (0.08)a	4.73 (0.08)a	4.71 (0.04)b
Average	4.52 (0.06)a	4.65 (0.06)a	4.74 (0.06)a	4.56 (0.06)a	
Whorl 1					
Spring	4.53 (0.08)a	4.46 (0.08)ab	4.43 (0.07)ab	4.27 (0.07)b	4.42 (0.04)a
Summer	4.46 (0.07)a	4.49 (0.07)a	4.74 (0.07)b	4.77 (0.07)b	4.61 (0.04)b
Average	4.49 (0.05)a	4.48 (0.05)a	4.58 (0.05)a	4.52 (0.05)a	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha=0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-9. Effects of Defoliation Intensity and Season on Average Width of Douglas-fir Subdominant Twigs August, 1990.

	Defoliation Intensity				
Season	0%	25%	50%	75%	Average
		[1] Whorl 3			
Spring	5.27 (0.05)ab	5.40 (0.05)a	5.39 (0.05)a	5.15 (0.05)b	5.30 (0.02)a
Summer	5.30 (0.05)ab	5.37 (0.05)b	5.20 (0.05)a	5.37 (0.05)b	5.31 (0.02)a
Average	5.28 (0.03)a	5.39 (0.04)a	5.29 (0.03)a	5.26 (0.03)a	
		Whorl 2			
Spring	5.02 (0.07)a	5.03 (0.07)a	5.02 (0.07)a	4.79 (0.07)a	4.96 (0.03)a
Summer	5.11 (0.07)a	4.99 (0.07)a	4.98 (0.07)a	5.00 (0.07)a	5.02 (0.03)a
Average	5.06 (0.05)a	5.01 (0.05)a	5.00 (0.05)a	4.90 (0.05)a	
		Whorl 1			
Spring	4.80 (0.07)a	5.13 (0.07)b	4.83 (0.07)a	4.69 (0.07)a	4.86 (0.03)a
Summer	4.90 (0.07)a	4.86 (0.07)a	4.77 (0.07)a	4.84 (0.07)a	4.84 (0.03)a
Average	4.85 (0.05)ab	4.99 (0.05)b	4.80 (0.05)a	4.76 (0.05)a	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha = 0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Table 3-10. Effects of Defoliation Intensity and Season on Number of Douglas-fir Twigs August, 1990.

	Defoliation Intensity				
Season	0%	25%	50%	75%	Average
			[1] *Whorl 4*		
Spring	30.4 (3.0)a	37.6 (3.1)a	29.4 (2.9)a	31.8 (3.0)a	32.3 (1.5)a
Summer	40.4 (3.0)a	34.4 (2.9)a	32.3 (2.9)a	30.7 (2.9)a	34.5 (1.5)a
Average	35.4 (2.1)a	36.0 (2.1)a	30.8 (2.1)a	31.3 (2.1)a	
			Whorl 3		
Spring	125.1 (8.6)a	142.8 (8.8)a	122.1 (8.3)a	146.3 (8.4)a	134.1 (4.2)a
Summer	145.8 (8.4)ab	167.5 (8.3)a	145.4 (8.4)ab	136.0 (8.3)b	148.7 (4.2)b
Average	135.4 (5.9)a	155.2 (6.0)a	133.7 (5.9)a	141.2 (5.9)a	
			Whorl 2		
Spring	369.1 (19.2)a	321.4 (19.6)a	238.2 (18.6)b	261.0 (18.8)b	297.4 (9.4)a
Summer	389.9 (18.8)a	404.4 (18.6)a	322.3 (18.7)b	287.1 (18.6)b	350.9 (9.4)b
Average	379.5 (13.2)a	362.9 (13.5)a	280.2 (13.2)b	274.1 (13.3)b	
			Whorl 1		
Spring	445.4 (34.7)a	425.8 (35.5)a	365.9 (33.7)a	330.8 (34.2)a	392.0 (17.0)a
Summer	426.3 (34.0)a	400.5 (33.6)a	367.8 (33.8)a	358.6 (33.6)a	388.3 (17.0)a
Average	435.9 (23.8)a	413.2 (24.3)a	366.9 (24.0)a	344.7 (24.0)a	

[1] Whorl Number: First whorl is the one closest to the ground.
Means within a row followed by the same letter do not differ ($\alpha = 0.05$, Fisher's Protected LSD). Standard error values are shown in parentheses.

Conclusions

The results indicated a gradient of response in area, length, width of dominants and subdominants and number of twigs within the crown. Little effects of intensity or season of defoliation on area of dominant twigs were observed two years after defoliation. This indicated that defoliation effects were short term. Length of dominant twigs followed the same trend as area, which reflects that the response of twig area is mainly attributed to change of twig length. Spring defoliation affected seedlings more than summer defoliation. Width of dominant twigs was not affected by any treatment two years after defoliation. Newly produced whorls produced dominant twigs which showed complete recovery from defoliation two years after defoliation.

Subdominant twigs were generally more sensitive to defoliation than dominant twigs and they continued to respond for two years after defoliation. Subdominant twigs can be used as a useful indicator to study tree stress. Similar to dominants, length and width of subdominant twigs were smaller for spring compared to summer defoliated trees.

Number of twigs was linearly inversely proportional to the level of defoliation intensity in 1989. Intensity had little effect on number of twigs in 1990. Priority for photosynthate allocation affects tree response to defoliation. Generally, young Douglas-fir has higher photosynthate allocation priority for dominants and number of twigs than subdominant twigs. Number of twigs in newly produced whorls was not affected by defoliation, which indicates that future growth potential was maintained. Twenty five percent defoliation has little or no effect on tree growth. Seventy five percent defoliation was more detrimental than other levels, yet young Douglas-fir was very resilient and can withstand even higher levels of defoliations.

Under the most severe treatment (75% defoliation in spring), a laterally defoliated Douglas-fir tree showed a reduction of 4% in height, 8 % in diameter, and 15% in canopy area compared to the control. This suggests that prior to defoliation Douglas-fir was operating below its maximum efficiency. A defoliated tree is also characterized by having fewer twigs, especially in its central part. Opening the canopy may have allowed better light penetration to the interior canopy.

Literature Cited

Bassman, J., W. Myers, D. Dickmann and L. Wilson. 1982. Effects of simulated insect damage on early growth of nursery-grown hybrid poplars in northern Wisconsin. Can. J. For. Res. 12:1-9.

Bernard-Dagan, C. 1988. Seasonal Variations in Energy Sources and Biosynthesis of Terpenes in Maritime Pine. Ed. by Mattson, W., J. Levieux, C. Bernard-Dagan, pp. 93-113. Mechanisms of Woody plants Defenses Against Insects Search for Pattern. Springer-Verlag. New York.

Bruce, D. 1956. Effect of defoliation on growth of longleaf pine seedlings. Forest. Sci. 2: 31-35.

Cannell, M. G. R., S. Thompson, and R. lines. 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. Ed. by M.G.R. Cannell and F.T. Last, pp. 173-205. Tree Physiology and Yield Improvement. Institute of Terrestrial Ecology, Scotland. Academic Press, London.

Corliss, J. F., and C. T. Dyrness. 1965. A detailed soil-vegetation survey of the Alsea area in the Oregon Coast Range. P. 457-483. In: C.T. Youngberg (ed.).Forest soil relationships in North America. Oregon State Univ. Press, Corvallis.

Corliss, J. F. 1973. Soil survey - Alsea area, Oregon. U. S. Govt. Printing Office, Washington, D.C.

Craighead, F. C. 1940. Some effects of artificial defoliation on pine and larch. J. of Forestry 38:885-888.

Crouch, G. L. 1968. Spring-season deer browsing of Douglas-fir on the capitol forest in western washington. US Forest Service Research Note. PNW-84.

Ericsson, A., S. Larsson, and O. Tenow. 1980. Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pine. J. of Appl. Ecol. 17:747-76

Freeland, R. O. 1952. Effect of age of leaves upon the rate of photosynthesis in some conifers. Plant Physiology 27:685-690.

Hartwell, H. D. 1973. Effect of deer browsing on height growth of Douglas-fir trees. Dept. of Nat. Res. Notes No. 5.

Hughes, R. H. 1976. Response of planted south Florida slash pine to simulated cattle damage. J. Range Manage. 29:198-210.

Kozlowski, T. T. 1969. Tree physiology and forest pests. J. of Forestry. 67:118-122.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Kulman, H. M. 1965. Effects of artificial defoliation of pine on subsequent shoot and needle growth. Forest Sci. 11:90-98.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Ann. Rev. of Ent. 16:289-324.

Larson, P. R., J. C. Gordon. 1969. Leaf development, photosynthesis, and C^{14} distribution in Populus deltoides seedlings. Am. J. Bot. 56:1058-66.

Neter, J., and W. Wasserman. 1989. Applied linear statistical models. Richard D. Irwin, Inc., Homewood,Il.

O' Neil, L. C. 1962. Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamn.). Can. J. of Botany 40:273-280.

Owens, J. N. 1968. Initiation and development of leaves in Douglas-fir. Can. J. of Botany 46:271-278.

Rook, D. A. and Whyte, A. G. D. 1976. Partial defoliation and growth of 5-year-old radiata pine. New Zealand Journal of Forestry Science, 6:40-56.

SAS Institute Inc. 1990. SAS/STAT Guide for personal computers. Version 6.03 ed. SAS Institute Inc., Cary, NC.

Sharrow, S. H., W. C. Leininger and B. Rhodes. 1989. Sheep grazing as a silvicultural tool to suppress brush. J. Range Manage. 42:2-4.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods. 8th Edition. The Iowa State Univer. Press, Ames, Iowa.

Steel, R. G. O. and J. H. Torrie. 1980. Principles and procedures of statistics. Second edition. McGraw-Hill book company. New York.

Wargo, P. M. 1978. Insects have defoliated my tree-now what's going to happen?. J. of Arboriculture 4(8):169-175.

Waring, P. F., and Patrick, J. 1975. Source-sink relations and the partition of assimilates in the plant. In 'Photosynthesis and Productivity in Different Environments' (J. P. Cooper, ed), IBP, Vol. 3, pp.481-499. Cambridge Univ. Press, London and New York.

Waring, R. H. 1987. Characteristics of trees predisposed to die. BioScience, 37:569-574.

Bibliography

Alejandro-Castro, M. 1988. Influence of cattle grazing and forage seeding on establishment of conifers in southwest Oregon. M.S. thesis, Department of Rangeland Resources, Oregon state University, Corvallis.

Allen, R. M. 1955. Foliage treatments improve survival of longleaf pine plantings. J. of Forestry. 53:724-727.

Barnett, J. P. 1984. Top pruning and needle clipping of container-grown southern pine seedlings. USDA Forest Service-Southern Region, New Orleans Louisiana. P. 39-45.

Bassman, J., W. Myers, D. Dickmann and L. Wilson. 1982. Effects of simulated insect damage on early growth of nursery-grown hybrid poplars in northern Wisconsin. Can. J. For. Res. 12:1-9.

Bassman, J., D. Dickmann 1982. Effects of defoliation in the developing leaf zone on young Populus X euramericana plants. I. Photosynthetic physiology, growth, and dry weight partitioning. Forest Sci. 28:599-612.

Beal, J. A. 1942. Mortality of reproduction defoliated by the red-headed pine sawfly (*Neodiprion lecontei* Fitch). J. of Forestry 40:562-563.

Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. The Am. Nat. 127:878-892.

Benoit, P. and R. Blais 1988. The effect of defoliation by the larch casebearer on the radial growth of tamarack. Forestry chronicle 64:190-192.

Bernard-Dagan, C. 1988. Seasonal Variations in Energy Sources and Biosynthesis of Terpenes in Maritime Pine. Ed. by Mattson, W., J. Levieux, C. Bernard-Dagan, pp. 93-113. Mechanisms of Woody plants Defenses Against Insects Search for Pattern. Springer-Verlag. New York.

Berryman, A. A. 1986. Towards a united theory of plant defense. In: Mechanisms of Woody Plants Defenses Against Insects Search for Pattern (Mattson, W. J., J. Levieux, and Bernard-Dagan, C. ed.) Springer-Verlag. New York. pp. 39-55.

Blais, J. R. 1958. Effects of defoliation by spruce budworm (*Choristoneura fumiferana* Clem.) on radial growth at breast height of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss.). Forestry Chronicle :39-47.

Britton, R. J. 1988. Physiological effects of natural and artificial defoliation on the growth of young crops of lodgepole pine. Forestry 61:166-175.

Brown, G. S. 1962. The importance of stand density in pruning prescriptions. Empire Forest. Rev. 41:246-257.

Bruce, D. 1956. Effect of defoliation on growth of longleaf pine seedlings. Forest. Sci. 2: 31-35.

Burger, H. 1951. Pruning, needle-stripping and increment of young spruce and pine. (German) Mitt. Forstl. VersAnstl, Mariabrunn No. 47:8-16. (Forest. Abstr. 13 No. 156).

Cannell, M. G. R., S. Thompson, and R. lines. 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. Ed. by M.G.R. Cannell and F.T. Last, pp. 173-205. Tree Physiology and Yield Improvement. Institute of Terrestrial Ecology, Scotland. Academic Press, London.

Corliss, J. F., and C. T. Dyrness. 1965. A detailed soil-vegetation survey of the Alsea area in the Oregon Coast Range. P. 457-483. In: C.T. Youngberg (ed.).Forest soil relationships in North America. Oregon State Univ. Press, Corvallis.

Corliss, J. F. 1973. Soil survey - Alsea area, Oregon. U. S. Govt. Printing Office, Washington, D.C.

Cown, D. J. 1973. Effect of severe thinning and pruning treatments on the intrinsic wood properties of young radiata pine. N. Z. J1, For Sci. 3:379-389.

Craighead, F. C. 1940. Some effects of artificial defoliation on pine and larch. J. of Forestry 38:885-888.

Crouch, G. L. 1968. Spring-season deer browsing of Douglas-fir on the capitol forest in western washington. US Forest Service Research Note. PNW-84.

Derr, H. J. 1963. Needle clipping retards growth of planted longleaf pine. U.S Dept. Agr. Service. Tree Planter's Notes 57:31-33.

Dimock, E. J. 1970. Ten-year height growth of Douglas-fir damaged by Hare and deer. J. of Forestry :285-288.

Doescher, P. S., S. D. Tesch and W. E. Drewien 1989. Water relations and growth of conifer seedlings during three years of cattle grazing on Southwest Oregon plantation. Northwest Sci. 63:232-240.

Doescher, P. S., M. Alejandro 1985. Cattle and establishment of conifer seedlings. Preliminary findings for southwest Oregon. P. 7-10 in Spec. Rep. 743. Agric Exp. Stn., Oreg. State Univ., Corvallis.

Doescher, P. S., S. D. Tesch and M. Alejandro 1987. Livestock grazing: A silvicultural tool for plantation establishment. J. of Forestry 85:29-37.

Emmingham, W. H. 1977. Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. Can. J. For. Res. 7:154-164.

Ericsson, A., S. Larsson, and O. Tenow. 1980. Effects of early and late season defoliation on growth and carbohydrate dynamics in Scots pine. J. of Appl. Ecol. 17:747-76

Ericsson, A. Hehhqvist, C., Langstrom, B., Lasson, S. and Tenow, O. 1985. Effects on growth of simulated and induced shoot pruning by *Tomicus piniperda* as related to carbohydrate and nitrogen dynamics in Scots pine. J. appl. Ecol. 22:105-124.

Evans, G. C. 1972. The quantitative analysis of plant growth. Univ. of California Press Berkeley.

Freeland, R. O. 1952. Effect of age of leaves upon the rate of photosynthesis in some conifers. Plant Physiology 27:685-690.

Gillingham, A. Gg., B. K. Klomp, and S. E. Peterson. 1976. Stock and pasture management for establishment of radiata pine in farmland. P.38-51. In:Proc. N. Z. Grassl. Assoc.

Graham, S. A. and F. B. Knight 1965. Principles of Forest Entomology. (4th Ed.). McGraw-Hill Book Co., New York. 417 p.

Graham, S. A. 1929. Principles of Forest Entomology. (4th Ed.). McGraw-Hill Book Co., New York. 339 p.

Graham, S. A. 1952. Forest Entomology, McGraw-Hill Book Co., Inc.,New York.

Gehring, C. A. and T. G. Whitham. 1991. Herbivore-driven mycorrhizal mutualism in insect-susceptible pinyon pine. Nature 353:556-557.

Hall, F. C., D. W. Hedrick and Keniston R. F. 1959. Grazing and Douglas-fir establishment in the Oregon white oak type. J. of Forestry 57:98-103.

Hartwell, H. D. 1973b. A comparison of large and small Douglas-fir nursery stock outplanted in potential wildlife damage areas. Dept. of Nat. Res. Notes No. 6

Hartwell, H. D. 1973a. Effect of deer browsing on height growth of Douglas-fir trees. Dept. of Nat. Res. Notes No. 5.

Hartwell, H. D. 1973b. A comparison of large and small Douglas-fir nursery stock outplanted in potential wildlife damage areas. Dept. of Nat. Res. Notes No. 6

Hedrick, D. W. and R. F. Keniston 1966. Grazing and Douglas-fir growth in the Oregon white oak type. J. of Forestry 64:735-738.

Hill, R. R. 1917. Effects of grazing upon western yellow-pine reproduction in the national forests of Arizona and New Mexico. Bull. No. 580, U.S. Dept. of Agric., Washington, D.C.

Hodgson, J. 1979. Nomenclature and definitions in grazing studies. Grass and Forage Sci. 34:11-18.

Hoshino, M., T. Shinjo and K. Sato. 1988. Utilization of *Avicennia marina* Vierh. as feed for animals. 1. Effect of method and frequency of cutting on the yield and survival of *A. marina*. Japanese J. of Tropical Agric. 32:223-227.

Hughes, R. H. 1976. Response of planted south Florida slash pine to simulated cattle damage. J. Range Manage. 29:198-210.

Kamilovski, M. 1966. Determining the best time to destroy defoliators of poplar. God. Zborn. Zemi. Sum. Fak. Univ. Skopje No. 19 157-86. (Forest. Abstr. 29 No. 2599).

Karl, M. 1991. Effects of prescribed cattle grazing on reforestation in Oregon's Southern Cascades. Ph. D. Diss., Dept. of Rangeland Resources, Oregon State Univ., Corvallis.

Karl, M. 1991. Effects of prescribed cattle grazing on reforestation in Oregon's Southern Cascades. Ph. D. Diss., Dept. of Rangeland Resources, Oregon State Univ., Corvallis.

Keller, R. and F. Thiercelin. 1984. Pruning of plantations of Norway spruce and Douglas-fir. Revue Forestiere Francaise 36:289-302.

Knight, F. B. and Heikknen H. J. 1980. Principles of Forest Entomology. (5th Ed.). McGraw-Hill Book Co., New York. 461 p.

Kozlowski, T. T. 1969. Tree physiology and forest pests. J. of Forestry. 67:118-122.

Kozlowski, T. T. 1971. Growth and Development of Trees. Vol. 2. Academic Press, New York.

Kozlowski, T. T., Kramer, P. J. and S. G. Pallardy. 1991. Physiological Ecology Woody Plants. Academic Press, Inc. San Diego, California 92101. 657 p.

Kozlowski, T. T., and C. H. Winget. 1964. The role of reserves in leaves, branches, stems and roots on shoot growth of red pine. Am. J. Bot. 51:522-29.

Kramer, P. J., and T. H. Wetmore. 1943. Effects of defoliation on cold resistance and diameter growth of broad-leaved evergreens. Am. J. Bot. 30:428-31.

Kramer, P. J. and T. T. Kozlowski. 1960. Physiology of trees. New York:McGraw-Hill Book Co., 642 p.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Krueger, W. C. 1983. Cattle grazing in managed forests, p. 29-41. In: B. F. Roche and D. M. Baumgartner (eds.), Proc. of Forestland Grazing Symposium, Washington State Univ., Pullman.

Krueger, W. C. 1987. Pacific Northwest forest plantations and livestock grazing. J. of Forestry 85:30-31.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Ann. Rev. of Ent. 16:289-324.

Kulman, H. M. 1965. Effects of artificial defoliation of pine on subsequent shoot and needle growth. Forest Sci. 11:90-98.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Ann. Rev. of Ent. 16:289-324.

Lane, R. D. 1963. Artificial defoliation of eastern white pine Duplicates some effects of chlorotic dwarf disease. US Forest Service, Research Note CS-16 Central States Exp. Station. Columbus, Ohio. p.6.

Langdon, O. G. 1955. Clipping needles adversely affects survival of south Florida slash pines. U.S. Dept. Agr. Forest. Serv., Southeast Forest. Exp. St. Res. Note 74,

Larson, P. R., J. C. Gordon. 1969. Leaf development, photosynthesis, and C^{14} distribution in Populus deltoides seedlings. Am. J. Bot. 56:1058-66.

Ledig, F. T. 1974. Concepts of growth analysis. P.166-182 in Proc. 3rd North Am. For. Bio. workshop. Coll. of For. and Natural Resource. Colorado State Univ., Fort Collins.

Leininger, W. C. 1984. Silvicultural impacts of sheep grazing in Oregon's Coast Range. Ph.D. Dess., Oreg. State Univ., Corvallis. 203 p.

Leininger, W. C. and S. H. Sharrow 1989. Seasonal browsing of Douglas-fir seedlings by sheep. Western J. of Appl. Forestry. 4:73-76.

Leininger, W. C. 1983. Silvicultural impacts of sheep grazing in Oregon's Coast Range. Ph.D. Dess., Oreg. State Univ., Corvallis. 203 p.

Lewis, C. E. 1980. Simulating cattle injury to planted slash pine: defoliation. J. Range Manage. 33:345-348.

Lewis, C. E. 1980a. Simulating cattle injury to planted slash pine: defoliation. J. Range Manage. 33:345-348.

Lewis, C. E. 1980b. Simulating cattle injury to planted slash pine: Combinations of defoliation, browsing, and trampling. J. Range Manage. 33:340-345.

Linzon, S. N. 1958. The effect of artificial defoliation of various ages of leaves upon white pine growth. Forestry Chronicle 34:50-56.

Madgwick, H. A. I. 1975. Effects of partial defoliation on the growth of *Liriodendron tulipifera* L. seedlings. Ann. Bot. 39:1111-1115.

Magnoler, A. and A. Cambini. 1970. Effects of artificial defoliation on the growth of cork oak. Forest Sc. 16:364-366.

McDonald, P. M. 1986. Grasses in young conifer plantations: hindrance and help. Northwest Sci. 60:271-78.

McGraw, J. B., K. W. Gottschalk, M. C. Vavrek. 1990. Interactive effects of resource availabilities and defoliation on photosynthesis, growth, and mortality of red oak seedlings. Tree Physiology 7:247-254.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

Moller, C. M. 1960. The influence of pruning on the growth of conifers. Forestry 33:37-53.

Neilsen, W. A. 1981. Effect of simulated browsing in survival and growth of Pinus radiata (D- Don) seedlings Aust. Forest Res 11: 47-53.

Neter, J., and W. Wasserman. 1989. Applied linear statistical models. Richard D. Irwin, Inc., Homewood,II.

O' Neil, L. C. 1962. Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamn.). Can. J. of Botany 40:273-280.

Owen, D. F. and Wiegert, R. G. 1976. Do consumers maximize plant fitness? Oikos 27:488-492.

Owens, J. N. 1968. Initiation and development of leaves in Douglas-fir. Can. J. of Botany 46:271-278.

Park, J. and R. L. Patton. 1975. Effects of drought and defoliation on some metabolites in roots of black oak seedlings. Can. J. For. Res. 5:457-463.

Parker, J. and Houston, D. 1971. Effects of repeated defoliation on root and root collar extractive of sugar maple trees. Forest Sci. 17:91-95.

Pearson, G. A. 1931. Recovery of western yellow pine seedlings from injury by grazing animals. J. For. 29:876-894.

Pollard, D. W. 1970. Effect of partial defoliation on leader growth. Bi-monthly research notes. Canadian Forestry Service, Dept. of Fisheries and Forestry. 26:10-11.

Redmond, D. R. 1959. Mortality of rootlets in balsam fir defoliated by the spruce budworm. Forest Sci. 4:64-69.

Rook, D. A. and Whyte, A. G. D. 1976. Partial defoliation and growth of 5-year-old radiata pine. New Zealand Journal of Forestry Science, 6:40-56.

Roy, D. F. 1960. Deer browsing and Douglas-fir Seedling growth in Northwestern California. J. of Forestry 58:518-522.

Running, S. W. 1976. Environmental control of leaf water conductance in conifers. Can. J. of For. Res. 6:104-112.

SAS Institute Inc. 1990. SAS/STAT Guide for personal computers. Version 6.03 ed. SAS Institute Inc., Cary, NC.

Sharrow, S. H., W. C. Leininger 1983. Sheep as a silvicultural tool in coastal Douglas-fir forest. P. 219-232 in D.D. Hannaway (ed.), Foothills for food and forests. oregon State Univ., Coll. Agric. Sci. Symp. Series #2. Timber Press, Beaverton, Or.

Sharrow, S. H., W. C. Leininger and B. Rhodes 1989. Sheep grazing as a silvicultural tool to suppress brush. J. Range Manage. 42:2-4.

Sharrow, S. H., W. C. Leininger and K. A. Osman. 1991. Sheep grazing effects on Coastal Douglas-fir forest growth: a ten year perspective. Forest Ecol. and Manage. (in press).

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods. 8th Edition. The Iowa State Univer. Press, Ames, Iowa.

Steel, R. G. O. and J. H. Torrie. 1980. Principles and procedures of statistics. Second edition. McGraw-Hill book company. New York.

Turner, N. C. 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil:339-366.

Verkaar, H. J. 1988. Are defoliators beneficial for their host plants in terrestrial ecosystems - a review? Acta Botanica Neerlandica 37:137-152.

Wareing, P. F., M. M. Khalifa and K. J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220:453-457.

Wargo, P. M. 1978. Insects have defoliated my tree-now what's going to happen?. J. of Arboriculture 4(8):169-175.

Waring, R. H. 1987. Characteristics of trees predisposed to die. BioScience, 37:569-574.

Waring, P. F., and Patrick, J. 1975. Source-sink relations and the partition of assimilates in the plant. In 'Photosynthesis and Productivity in Different Environments' (J. P. Cooper, ed), IBP, Vol. 3, pp.481-499. Cambridge Univ. Press, London and New York.

Waring, R. H., and B. D. Cleary. 1967. Plant moisture stress: Evaluation by pressure bomb. Science 155:1248-1254.

Appendix

Appendix Table 1. Summary Table for Responses of Different Tree Parts to Defoliation During 1988-1990.

Year	Base Diameter	T-Diameter [1]	Canopy	Height	M (Ψ)
			Absolute Values		
1988	SE	---	IN, SE	SE	SE X DATE
1989	IN	IN	IN	SE	IN
1990	IN	IN	IN	SE	---
			Relative Growth Rates		
1988	NS	---	IN, SE	SE	---
1989	IN	---	NS	NS	---
1990	NS	---	NS	NS	---

(1) Diameter measured at the base of the terminal leader.
SE: Season; IN: Intensity of defoliation; NS: Not significant
M (Ψ): Mid-day xylem potential.
Treatments shown were significant at ($\alpha = 0.05$).

Appendix Table 2. Summary Table for Responses of Different Whorls to Defoliation During 1989-1990.

	Whorl Number (1)			
Year	1	2	3	4
Dominant Twigs				
1989				
Length	SE,IN	SE,IN,X	SE,IN,X	
Width	SE,X	SE	SE	
Area	SE, IN, X	SE, IN, X	SE, IN, X	
# of Twigs	SE, IN	IN	NS	
1990				
Length	IN	IN, X	IN	NS
Width	NS	NS	NS	NS
Area	NS	X	NS	NS
# of Twigs	NS	SE, IN	SE	NS
Subdominant Twigs				
1989				
Length	SE	SE		
Width	SE,X	SE		
Area	SE, X	SE		
1990				
Length	SE	SE,IN	SE,IN	
Width	IN,X	NS	X	
Area	NS	SE, IN	SE, IN	

(1) Whorl Number: First whorl is the one closest to the ground.
SE:Season; IN:Intensity of defoliation; X:Interaction between Season and intensity.
Treatments shown were significant at ($\alpha = 0.05$) using Fisher's Protected LSD.